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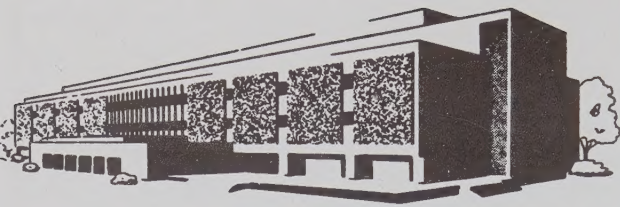
DAVID DUDGEON

PATTERNS AND PROCESSES IN STREAM ECOLOGY


**A synoptic review of Hong Kong
running waters**



STUTTGART
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und ihren Nachbargebieten

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Patterns and processes in stream ecology

A synoptic review of Hong Kong running waters

By

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With 40 figures and 9 tables



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Preface

There are at least two ways of approaching the study of nature. One tactic is to investigate a habitat or any convenient local environment with the aim of producing an inventory of the type of organisms found there, preferably with some indication of their relative abundance or population densities. The second approach concentrates upon what the organisms are doing in the habitat, and might involve measuring attributes of groups of animals which tend to exhibit similar interactions or use the same resources – such as predators or the animals which eat plant foliage – but which are not necessarily closely related. In the first case we are asking a descriptive question: “Which organisms live in the habitat?” We label them using a scientific name, but without additional information this does not provide us with any understanding of the habitat. In the second case we ask: “What are the organisms doing?” – a functional question. The two approaches are complementary, with the descriptive approach often preceding the functional one, but they are nonetheless distinct. The ecological literature exhibits a clear dichotomy between these approaches, and books tend to focus on either one or the other. If the main goal is to introduce the reader to descriptive studies, an identification manual (with keys and line drawings) would be the usual publication. If the functional approach is adopted, an introduction to ecological patterns and the processes bringing them about would be the subject of the text.

Rather little is known about the ecology of seasonal tropical freshwaters in general, and Hong Kong’s freshwaters in particular. Moreover, there has been no attempt to synthesize the material that is available in the primary scientific literature. This book outlines the main ecological patterns, both temporal and spatial, which characterize Hong Kong streams and rivers. Attempts are made to account for the observed patterns by recourse to characteristics of the populations that comprise freshwater communities, and the properties and interactions of the individual organisms constituting those populations. Attention is centred upon animals although they are not considered to the exclusion of plants. The intention here has not been to produce an identification guide; indeed, it is worth emphasizing that our taxonomic knowledge of Hong Kong running-water fauna is restricted, as reflected in this text by the use of letters or numbers to designate as yet undescribed species within genera.

The science of running-water ecology has developed rapidly over the past two decades, and it is no longer possible for a single volume to do justice to the diversity of endeavours included in this subject. There are numerous controversies and questions associated with the workings of stream and river habitats in temperate regions; our knowledge of equivalent tropical habitats is so scanty that it is difficult to know which questions to ask. For this reason, it is necessary to rely on the results of investigations undertaken in temperate regions to assist in interpreting some of

the patterns and processes occurring in Hong Kong streams. While the reader (and this writer) may wish that there was more data available from tropical running waters, the use of literature from north temperate or antipodean sources should allow Hong Kong streams to be viewed in something approaching a global perspective.

I Communities

River zonation and classification schemes

The dominant physical feature of any stream is the unidirectional flow of water from the headwaters to the mouth. Stream organisms must contend with this constant downhill flow, and water current is the major factor underlying their distribution and abundance. Indeed, the stream can be thought of as a one-way channel along which water, as well as suspended and dissolved materials, both organic and inorganic, travel. The persistence of the organisms comprising the stream community depends on an ability to collect and retain transported materials which serve either as food for animals, a substrate for microbes, or as nutrients for plant growth. The community structure in any given section of stream will therefore reflect the interaction between the biological potential for collection and retention of organic matter and the physical conditions prevailing at that site. Because the physical characteristics of a stream change along a continuous gradient from headwaters to mouth, so too will the stream community alter and thereby exhibit a pattern of longitudinal zonation.

Man has long known of the association of particular animals and plants with different river reaches, and the use of streams as a source of food must have spurred the first attempts at classification of river zones. The earliest formalized schemes, based mainly on the presence of dominant fish species, originated in Germany towards the end of the last century and were later extended to, or modified to apply to, other parts of Continental Europe. The general concept of river zonation had been accepted widely by the mid-1920s, and most subsequent studies involved fine-tuning the German river-zonation scheme to match local circumstances (HYNES 1970; HAWKES 1975). Such research highlighted one significant drawback to the use of characteristic fishes to identify different river zones: for geographic or historic reasons the key species might be absent or have a restricted distribution in a given region or country. In addition, transitions in fish community composition did not always occur abruptly, permitting the identification of discrete zones, but instead involved gradual changes in species representation. Further difficulties arose when it became clear that downstream changes in some elements of the stream community (such as the benthic invertebrates) did not occur in parallel with transitions from one fish zone to the next (HAWKES 1975). Clearly, a fuller appreciation of the factors determining the distribution of individual species along the course of a river was needed before a complete understanding of longitudinal zonation could be attained.

It is now clear that lotic organisms are distributed in response to a complex of physical factors, the most important of which are current velocity, flow pattern and discharge, substratum characteristics (including particle size and complexity), temperature, and dissolved oxygen (HYNES 1970; STATZNER & HIGLER 1986).

Individual species respond uniquely to combinations of these factors, and thus their patterns of longitudinal zonation also differ. Accordingly, it is unrealistic to expect synchronized changes in the associations of fish, plants and invertebrates at well-defined boundaries along the physical continuum that constitutes the course of a river. Longitudinal changes in species composition may be used to partition a river into rather broad subdivisions, but we should not expect to be able to identify each zone with any great precision. One attempt to formulate a widely-applicable scheme involved division of rivers into upland rithron and lowland potamon regions (ILLIES 1961), based largely on temperature. Unfortunately, this scheme is subject to the vagaries of local climate and relief (HYNES 1970), and may not apply equally to all rivers within a single country (TOWNS 1979). Indeed, there may be little information in such a classification that could not be imparted by the use of the terms 'lowland' or 'floodplain' and 'upland', 'highland' or 'headwater' to describe the parts of a river system. Whatever scheme is used, each zone that is identified on the basis of species composition will include organisms with similar responses to physical factors, but need not include taxa which interact or are linked functionally. Without a functional basis, however, schemes of river zonation and classification can have little predictive value.

Functional classification of stream animals

Stream benthos the world over is dominated by immature insects, both in terms of numbers and species richness (HYNES 1970). The diversity of benthic communities, coupled with the difficulties of identifying species of larvae, have encouraged stream ecologists to develop a functional characterization of aquatic insects according to how they feed (CUMMINS 1973). While this scheme was developed for insects it is applicable, in principle, to other aquatic animals such as crabs, shrimps, snails and fishes. The approach is valid since variations in ecological parameters (distribution, trophic relations, growth rate) may be quite marked between different stages in the development of a given species, while different species in the same functional group are, by definition, similar. Functional classification of invertebrates also has the advantage of reducing the difficulty of dealing with taxonomic groups which are poorly known. Additional benefits include a simplification of community structural data, and thus a facilitation of pattern recognition in ecosystems.

The main functional feeding groups are:

- 1) Grazers and scrapers – herbivores feeding on periphyton (i.e. attached algae and associated material), including those which pierce plant tissues or cells and suck out fluids;
- 2) Shredders – detritivores feeding on coarse particles (especially decomposing leaf litter derived from the riparian zone), with a significant reliance on the associated microbes;
- 3) Collectors – feeding on fine (< 1 mm in size) particles (and associated microbes) suspended in the water (= filtering-collectors or filter-feeders) or deposited on the substratum (= collector-gatherers);
- 4) Predators – including those which swallow or engulf prey, and those which pierce their animal victims extracting cell and tissue fluids.

Clearly there is an overlap between functional groups, and some animals are best categorized as generalists, but a given age class tends to fall predominately into one functional group (CUMMINS 1973). Note also that because categories (e.g. filtering-collectors) are based on feeding mode, members may ingest both living and dead plant tissue. Nevertheless, the four functional components listed above do appear necessary for community stability in undisturbed streams and rivers (CUMMINS 1975). In running waters receiving organic enrichment (pollution) a fifth functional category – deposit-feeders – can be added to include those species ingesting fine bottom sediments and the organic material that they contain. Alternatively, these animals may be considered as specialized collector-gatherers.

A general classification of the trophic relations of macroinvertebrates in Hong Kong streams is given in Table 1. The categories used are broad, and generalizations included therein are likely to suffer from some exceptions due to the relatively small number of species whose trophic ecology has been well studied. Certain species exhibit more than one feeding mode (McSHAFFREY & McCafferty 1986, 1988), and feeding habits may change according to developmental stage or local circumstances: for example, *Brotia hainanensis* – a thiarid snail – can feed as a shredder or a grazer and is therefore assigned to a combined functional group. Other taxa, such as hydropsychid caddisflies, are primarily filter-feeders which sieve particles from the current with the aid of a silken capture net; nevertheless, they behave as predators when an animal is caught on the mesh.

Stream invertebrates play an important role in the consumption of reduced carbon compounds derived primarily from the surrounding land (allochthonous material), supplemented by autochthonous material produced by in-stream photosynthesis, and bring about their transformation and temporary storage as animal tissues or conversion (via respiration) into carbon dioxide. Shredders consume leaves, bark, and so on and, by the action of chewing and defecating, comminute the food material and produce fine particles that can be gathered or filtered by collectors (ANDERSON & SEDELL 1979; CUMMINS & KLUG 1979). Filter-feeders, in particular, use a variety of capture methods and a wide range of particle sizes are retained (WALLACE & MERRITT 1980). The faeces that collectors produce are generally only slightly smaller or larger than the food particles, and may be reingested by other collectors. Herbivores graze the plant stocks (generally algae) in the stream and produce faeces which can be taken up by collectors. Microbial colonization of invertebrate faecal pellets enhances their food value to collectors and may encourage coprophagy. This continued cycle of colonization and recolonization of detritus particles by micro-organisms (especially fungi), and their repeated ingestion and defaecation by collectors, can be viewed as an 'external rumen' (McLACHLAN 1978). Ultimately, the predators consume shredders, collectors and herbivores, so feeding indirectly upon the detritus and algae which has been assimilated by their prey (CUMMINS 1973, 1975).

In summary, streams and rivers are primarily flow-through systems, receiving all material passing through them from the surrounding landscape and exporting it downstream or mineralizing some organic inputs to completion. Members of the functional feeding groups act as interrelated temporary storage bins for organic compounds which are eventually converted to carbon dioxide. Linkages between the feeding groups are characterized by changes (usually decreases) in the size of particles, and the efficiency with which food is transferred between groups, together

Table 1. A preliminary functional feeding group classification of macroinvertebrate taxa in Hong Kong streams.

Annelida		Lepidoptera	
All Oligochaeta	D	Pyralidae	Sc
All Hirudinea	P	Trichoptera	
Mollusca		Rhyacophilidae	P
All Bivalvia	F	Glossosomatidae	Sc
Gastropoda		Hydroptilidae	Pr
Thiaridae	ShSc	Philopotamidae	F
Viviparidae	CoSc	Psychomyiidae	Co
Lymnaeidae	G	Xiphocentronidae	Co
Physidae	G/Sc	Polycentropodidae	P
Planorbidae	G	Pseudoneureclipsiidae	Co?
Ferrissiidae	CoSc	Ecnomidae	P
Crustacea		Hydropsychidae	F
Potamidae	Sh	Brachycentridae	CoSc
Parathelphusidae	P	Lepidostomatidae	Sh
Atyidae	Co	Odontoceridae	Sc
Palaemonidae	P	Helicopsychidae	Sc
Ephemeroptera		Calamoceratidae	Sh
Baetidae	CoSc	Leptoceridae	CoSc
Oligoneuriidae	F	Coleoptera	
Heptageniidae	CoSc	Gyrinidae	P
Ephemerellidae	CoSc	Haliplidae	Sc
Caenidae	CoSc	Dytiscidae	P
Leptophlebiidae	CoSc	Hydrophilidae	CoSc
Ephemeridae	Co	Hydraenidae	Co?
Prosopistomatidae	Sc	Psephenidae	Sc
Odonata		Dryopidae	CoSc
All Zygoptera	P	Helodidae	Co
All Anisoptera	P	Elmidae	CoSc
Plecoptera		Ptilodactylidae	Co
Nemouridae	CoSh	Diptera	
Leuctridae	Sh	Nymphomyiidae	CoSc
Perlidae	P	Tipulidae	Sh/P
Hemiptera: Heteroptera		Culicidae	Co/P
Hydrometridae	P	Psychodidae	Co
Veliidae	P	Ceratopogonidae	P
Gerridae	P	Chironomidae	
Belostomatidae	P	Tanypodinae	P
Nepidae	P	Orthocladinae	CoSc
Heterotrephidae	P	Chironominae	Co
Naucoridae	P	Simuliidae	F
Corixidae	Sc	Dixidae	Co
Notonectidae	P	Stratiomyidae	Co?
Megaloptera		Empididae	P
Corydalidae	P	Syrphidae	Co

Key: Co = collectors; Sh = shredders; F = filter-feeders; P = predators; Sc = scrapers; ShSc, CoSh, CoSc = mixed feeding modes (shredder-scaper, collector-shredder, etc); Sh/P, Co/P = alternative feeding modes (shredder or predator, collector or predator, etc); G = generalists; D = deposit-feeders; Pr = piercers of plant cells.

with the physical characteristics of a particular river reach, will determine the magnitude of downstream loss of organic matter.

The River Continuum Concept

Can an appreciation of functional feeding groups and their interactions inform schemes of river zonation and classification? From headwaters to mouth, the physical variables within a river system present a continuous gradient; the River Continuum Concept (VANNOTE et al. 1980) conceptualizes the running-water system as a continuously integrating series of physical gradients and biological adjustments. Streams are seen as longitudinally-linked systems or continua in which downstream processes are linked to those upstream. Accordingly, predictable longitudinal variations in community organization should occur in response to varying hydrological and physical conditions, as well as changes in the resource base.

The River Continuum Concept has provided useful generalizations concerning the magnitude and variation over time and space of the organic matter supply, and the effects that this has on the structure of aquatic communities. By focusing on streams and rivers as integrated systems rather than discrete reaches, running-water ecology has begun the transformation from a descriptive to a predictive science. In essence, the Concept identifies broad characteristics of lotic communities which are roughly grouped according to size into headwaters, medium-sized streams and large rivers. Many headwater streams are influenced strongly by riparian vegetation which reduces autotrophic production by shading, and contributes large amounts of allochthonous detritus. Shredders are hypothesized to be co-dominant with collectors in such streams, reflecting the importance of the riparian zone and the detritus derived from it.

As stream width increases and shading decreases, the reduced importance of the allochthonous litter input coincides with a greater significance of autochthonous primary production and the import of fine organic particles from upstream. Here scraper biomass is maximized, but collectors will also be numerous. The transition from headwaters, dependent on terrestrial inputs, to medium-sized rivers, relying on algal or aquatic macrophyte production, is reflected by a change in the ratio of gross primary productivity (P) to community respiration (R). The position at which the stream shifts from heterotrophic ($P/R < 1$) to autotrophic ($P/R > 1$) depends upon the degree of shading and thus the form and extent of the riparian vegetation (MINSHALL 1978).

Large rivers receive fine particulate organic matter from upstream and, although the shading effect of riparian vegetation is insignificant, primary production may be limited by water depth and turbidity; here the river may once again become heterotrophic ($P/R < 1$). There will be a general reduction in detrital particle size along with an increase in stream width and, as a result, collectors (especially filter-feeders) will dominate macroinvertebrate assemblages downstream (VANNOTE et al. 1980).

The River Continuum Concept views benthic communities as being structured so as to make efficient use of energy inputs, this feature arising from the tendency of individual species to exploit their environment by maximizing energy consump-

tion. Communities in natural streams are considered to be in dynamic equilibrium, resulting in food-processing strategies that involve minimum energy loss (VANNOTE et al. 1980). Indeed, the biological processing of detritus and its downstream transport by the current can be seen as competing, with members of the benthic community striving to maximize their ingestion of organic material before it is exported from the system.

Although the universality and some of the tenets of the River Continuum Concept remain to be evaluated (WINTERBOURN et al. 1981; LAKE et al. 1985; STATZNER & HIGLER 1985), with a greater emphasis placed upon mechanism rather than generalized description (WILEY et al. 1990), it remains a useful framework for comparing riverine ecosystems (MINSHALL et al. 1985; NAIMAN et al. 1987). In particular, the Concept has highlighted some central concerns in stream ecology, such as a greater realization of the critical linkage between the stream and its terrestrial setting (CUMMINS et al. 1989), the development of ideas on material cycling and dynamics in open systems (NEWBOLD et al. 1983a, 1983b; CUFFNEY et al. 1990), and a recognition of the importance of biotic interactions within the stream community (MINSHALL et al. 1985). It is in the light of these notions, that the following account of Hong Kong running waters is given.

General features of Hong Kong running waters

Hong Kong comprises the southern end of a mountain chain that was flooded by rising sea levels following the last period of glaciation approximately 6000 years ago. The landscape is therefore dominated by hills, and coastal plains are of limited extent. As a result, most streams have steep stony valleys with rather restricted sections of gently flowing water in the lower valleys. Exceptions to this generalization are the Rivers Beas, Indus and Ganges which drain into the Sham Chun River along the border with China. They flow through densely-populated (1000–3000 persons/km²) rural areas and whiteland close to burgeoning New Towns, and hence receive heavy pollution loads from agricultural and domestic sources.

Hong Kong's hills and peaks are composed of porphyries, fine-grained volcanics and coarse-grained granites or granitic rocks. Granites are susceptible to chemical weathering brought about by the alternation of hot, wet summers and cool, dry winters, and large areas of hillside are deeply decomposed. As a result, most streams cut deeply-incised valleys containing substantial deposits of colluvium. During the dry season, surface flow may disappear into the colluvium matrix to return again upon the onset of the summer monsoon.

Water chemistry in unpolluted Hong Kong streams reflects the igneous geology and soil characteristics. Hillside soils are thin (sometimes < 10 cm deep), but alluvial deposits have accumulated on coastal plains in the northwest New Territories. The natural hillside soils are acidic and poor in cations, consisting of red krasnozems and red-yellow podzols. As a consequence, stream waters are soft, slightly acidic and low in dissolved ions, with conductivities rarely exceeding 50 μ S/cm. Natural concentrations of ammonia and phosphates are generally considerably less than 1.0 mg/l, while potassium, calcium and nitrate levels are < 2.0 mg/l. Most metals occur at low levels (\leq 0.01 mg/l) except iron which may

reach concentrations of an order of magnitude higher. Sodium and chloride levels are rather variable depending on wind-blown salt and proximity to the sea. Silicate concentrations are naturally high (> 10 mg/l), reflecting the products of silicate hydrolysis associated with granitic rocks. A profusion of basic silicate compounds may explain the weakly acid pH (> 6.5) of streams draining acid ($pH < 5$) soils, because the soluble basic compounds will drain into the stream leaving the more acidic products of hydrolysis to accumulate in the soil (DUDGEON 1982a). Other characteristics of the hydrology of unpolluted Hong Kong streams include dissolved oxygen levels at or near saturation and five-day Biological Oxygen Demand (BOD_5) in the order of $0.4 - 1.0$ mg/l (DUDGEON 1982a).

Suspended solid loads (seston) vary among Hong Kong streams, reflecting both catchment vegetation and location along the river course. For example, water in the lower Lam Tsuen River during 1978–79 contained > 10 times more organic matter than the headwaters, much of which was attributable to algal (Chlorophyta) unicells, filamentous algae and aquatic macrophyte tissue (DUDGEON 1984a). By contrast, the bulk of suspended material in the upper course comprised diatoms and allochthonous detritus. Moreover, there was a constancy in the general composition of the seston at any one site although the magnitude of the suspended load varied seasonally (DUDGEON 1984a).

While there are clear downstream trends in seston composition in Hong Kong streams, little can be said in this regard concerning natural water chemistry. Downstream increases in nutrients are, however, not generally characteristic of running waters although, along with reductions in dissolved oxygen, they are a feature of most Hong Kong streams as a consequence of organic pollution. By contrast, undisturbed catchments tend to conserve nutrients (VITOUSEK 1977) and downstream dilution of dissolved substances can result from a decrease in the input area (i.e. the river bed and banks) in relation to the increasing size and volume of the lotic habitat; the inflow of extra water from tributaries may dilute the main stream further (GOLTERMAN 1975).

None of the rivers of any size in Hong Kong has escaped the effects of pollution, and it is impossible to consider patterns of longitudinal change and zonation without taking cognisance of that fact. The picture is complicated further by seasonal fluctuations in pollution loads which result from the diluting effect of increased stream discharge volumes between April and September when $> 80\%$ of the annual rainfall occurs. Nevertheless, investigations of the Lam Tsuen River, which is moderately polluted along part of its course, do give an insight into patterns of river zonation in Hong Kong although the picture that emerges from this example is some way from the ideal that would be presented by a pristine habitat.

Longitudinal zonation along the Lam Tsuen River

The river valley

The Lam Tsuen River is a sixth-order stream that drains a broadly circular catchment of some 18.5 km² situated west and inland of Tai Po (Fig. 1). The dendritic stream network has a density of 5.3 km/km², and the relief of the land –

the highest point in the watershed is at 800 m elevation – suggests severe hydrographs. The floor of the Lam Tsuen Valley is largely alluvium while the upper and western sides are composed of pyroclastic rocks and associated lavas; the lower eastern portion consists of igneous rock (Tai Po granodiorite) dating from the Jurassic era (ALLEN & STEPHENS 1971). The headwaters arise to the southwest of Tai Po on the slopes of Tai Mo Shan and are marked by a series of spectacular waterfalls. The river then flows through hillside shrubland and ravines cloaked in forest, and thence into cultivated land devoted to market gardening as well as pig and chicken rearing. Approximately 2.5 km from the original river mouth (now displaced by land reclamation), the course changes from a southwest-northeast to a northeast-southwest direction, the result of an old river capture. Further downstream, the flow is blocked by an inflatable fabridam from where water is pumped, via a series of tunnels, into Plover Cove Reservoir. Probably < 10% of the river water avoids this diversion, and in 1984 the course of the river below the dam was channelized – effectively destroying the flood-plain habitat. The account presented herein is based on information which predates that destruction.

Characterization of the river fauna

Prior to 1984, the Lam Tsuen River fauna was diverse, including animals of various habits from a range of phyla. Neustic forms were well-represented, comprising hemipteran bugs (suborder Heteroptera) as well as gyrrinid (whirligig) and certain dytiscid beetles. The Heteroptera include taxa dwelling on the surface film – Gerridae (water skaters), Veliidae, Hebridae, Hydrometridae and Mesoveliidae – as well as those such as *Diplonychus rusticum* (Belostomatidae), *Ranatra* sp. (Nepidae) and Notonectidae which hang suspended beneath the water surface. Some of these animals (the gerrid *Ptilomera tigrina* and the veliid *Rhagovelia* sp.) are characteristic of turbulent headwater sections, while *Enithares* and *Anisops* spp. (Notonectidae) occur in pools between such reaches. By contrast, *Microvelia donglasi* (Veliidae), mesoveliids, *Diplonychus*, and the gerrids *Limnogonus fossarum* and *Gerris* (*Aquarius*) *paludum insularis* are more typical of the quieter downstream waters where they may be associated with aquatic macrophytes. Most of these heteropteran bugs are carnivores which feed on insects that become trapped on the surface film; their habit is such that they straddle the boundary between land and water.

The nekton includes powerful swimmers which inhabit open water and are capable of moving against the current. In streams, this niche is occupied largely by fishes, although beetles (certain Dytiscidae and Hydrophilidae) swim freely in the water column in slow-flowing weedy reaches. There has never been a complete fish survey of any Hong Kong river, and knowledge of the ecology of many species is hampered because of this. Nevertheless, it is clear that certain species are typical of headwater sites in the Lam Tsuen River. They include the alga-eating homalopterid loaches *Pseudogastromyzon myersi* and *Liniparhomaloptera dispar*, as well as predatory gobies (*Tukugobius wui*) and loaches (*Noemacheilus fasciolatus* and *Oreonectes platycephalus*); the latter is confined largely to first- and second-order tributaries. Turbulent waters and rapid currents have forced these fishes to abandon the nektonic habit for a secondarily benthic way of life that has involved modification of the body, pelvic and (sometimes) pectoral fins. More typically nektonic, minnow-like fishes of stony upstream reaches inhabit pools, and include the cyprinids *Parazacco spilurus*, and

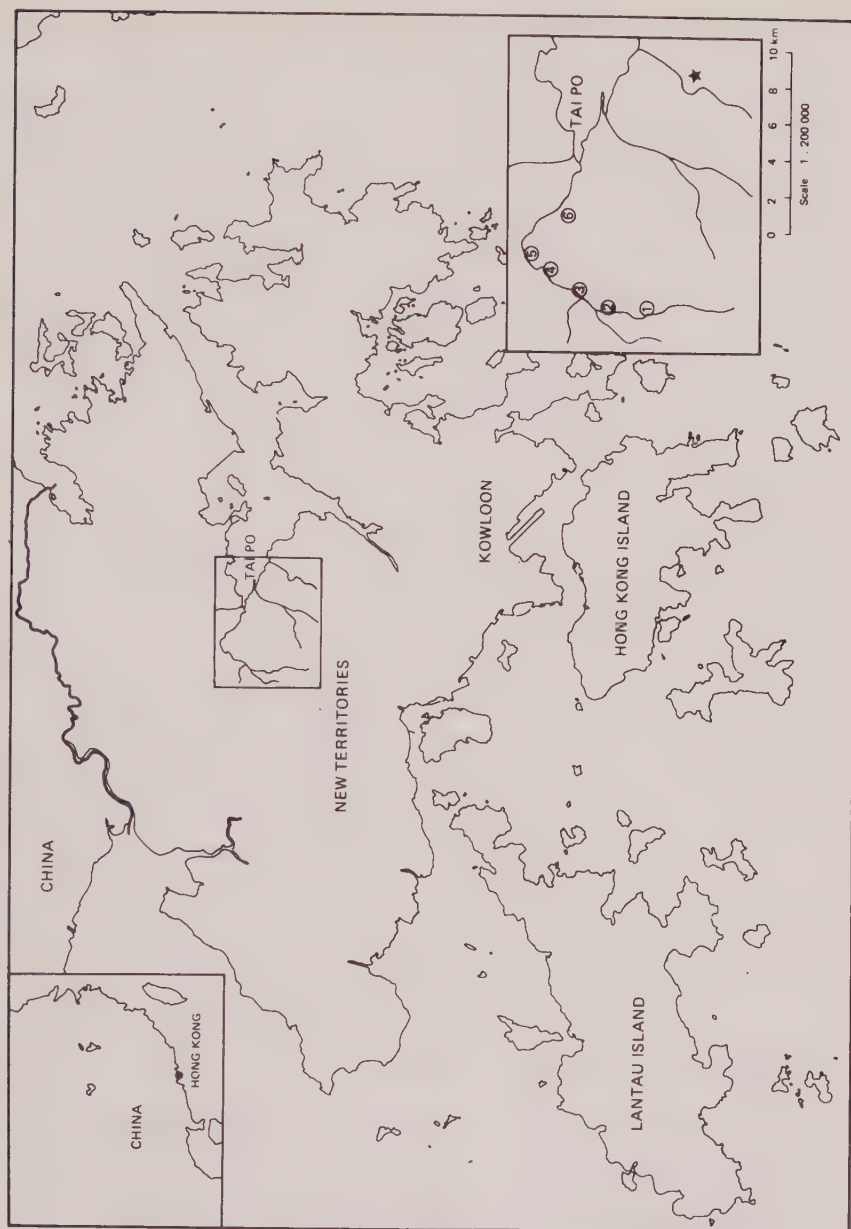


Fig. 1. Sketch map of the territory of Hong Kong, showing the location of Lam Tsuen River and (inset) the position of sampling sites 1-6; Tai Po Kau Forest Stream is indicated by a ★.

Nicholsicypris normanni. None of these animals tolerate organic pollution, and they are replaced by a different array of fishes, including exotic species, further downstream.

Native fishes characteristic of the lower reaches of Lam Tsuen River include the cobitid loach *Misgurnus* sp., the common carp *Cyprinus carpio*, the catfishes *Parasilurus* sp. (Siluridae) and *Clarius batrachus* (Clariidae), and the half-banded barb *Puntius semifasciolatus* and the minnow *Zacco platypus* (Cyprinidae). The yellow eel *Monopterus albus* (Synbranchidae) occurs in slow-flowing water supporting dense growths of aquatic macrophytes; it has an auxiliary intestinal respiratory organ and takes atmospheric air from the water surface. *Monopterus albus* shares the ability to breathe air with the paradise fish (*Macropodus opercularis*: Belontiidae), which has an accessory breathing apparatus in the head. Notwithstanding such respiratory adaptations, *Macropodus* is found in a range of freshwater habitats in addition to those where low levels of oxygen prevail.

In addition to native fishes, the lower course of the Lam Tsuen River is host to an array of exotic fishes. Among them is the African mouth-brooding cichlid or tilapia, *Oreochromis mossambicus*, which has spread across tropical latitudes as a result of its use in aquaculture, and the live-bearing Central American poeciliid fishes *Poecilia reticulata* (the guppy), *Gambusia affinis* (the mosquito fish), *Xiphophorus helleri* (the swordtail) and *X. variatus* (the variable platy). The biology and ecological effects of certain of these exotic species will be considered in some detail below (Part IV).

The benthic animals constitute the richest faunal assemblage in the Lam Tsuen River, and include planarians, annelid worms and leeches, gastropod and bivalve molluscs, decapod crustaceans (crabs and shrimps), and a predominance of amphibiotic insects. The latter comprise mayflies (Ephemeroptera), damselflies (Odonata: Zygoptera), dragonflies (Odonata: Anisoptera), stoneflies (Plecoptera), caddisflies (Trichoptera), beetles (Coleoptera) and true flies (Diptera), as well as a few moths (Lepidoptera: Pyralidae), riffle bugs (Hemiptera: Heteroptera: Naucoridae) and fish-flies (Megaloptera). Over 120 different taxa have been recorded from the bottom sediments alone but, because of the difficulty of separating the larvae of closely-related species, the actual total must be greater than this. The identification and taxonomy of most aquatic insects is based on the genital morphology of the adult males. For this reason, larvae cannot always be associated with named species, and it has sometimes been necessary to distinguish members of the same genus by a letter and/or number (e.g. *Baetis* T₃) rather than by a specific epithet. Most of the species so designated have yet to be described or named by systematists.

Benthos species richness declines along the Lam Tsuen River from headwaters to mouth, but total population densities generally increase (Table 2). These changes result from organic pollution in the lower course – revealed by seasonal and downstream changes in water quality (Fig. 2) – as well as natural transformations of the benthic environment, particularly differences in substratum characteristics along the river (DUDGEON 1984a). In essence, the size and variety of particles in the river bed are greater at upstream sites than downstream, where there are more fine-grained sediments. Benthic animals are intimately associated with the substratum, and their distribution and abundance is profoundly influenced by particle size (HYNES 1970; MINSHALL 1984). It is perhaps not surprising, therefore, that upstream sites with a variety of particles and a physically complex or heterogeneous substratum support a greater range of benthic species (Table 2). Further

Table 2. Taxonomic richness and population densities of benthic macroinvertebrates at six stations along the Lam Tsuen River, 1978-79.

Station no.	1	2	3
Total no. taxa	62	53	45
(range)	(39-50)	(35-40)	(18-39)
Mean no./m ²	3583	5277	121781
(range)	(2071-4931)	(2940-7937)	(41721-164668)

Station no.	4	5	6
Total no. taxa	36	32	19
(range)	(15-30)	(8-28)	(7-12)
Mean no./m ²	117193	167557	23927
(range)	(65638-248293)	(72762-389308)	(8183-40612)

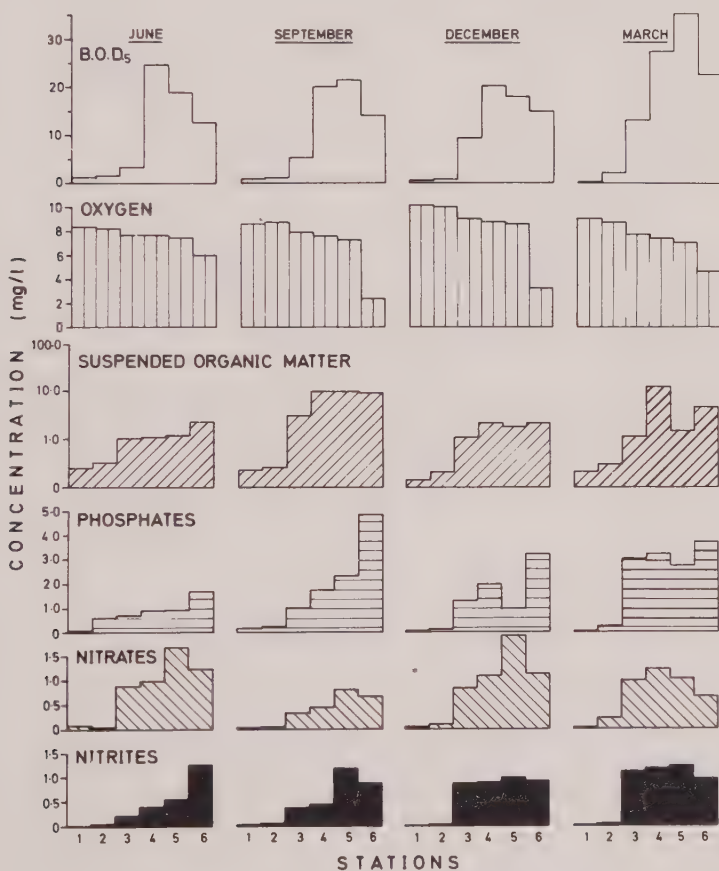


Fig. 2. Hydrological conditions prevailing at six stations along the Lam Tsuen River, 1978-79.

downstream, fine-grained particles deposited on the river bed cause a loss of habitat as they fill crevices or cavities between rocks and boulders which could have been occupied by burrowing animals. Moreover, the addition of fine organic particles to the river by polluters may smother the gills and feeding apparatus of some taxa. The effect on filtering-collectors can be especially marked as high concentrations of particles in the water clog the nets and filtering mechanisms by which these animals feed.

Although the diversity of benthic animals is reduced in the lower Lam Tsuen River, prior to 1984 this loss of species was compensated by the presence of trailing terrestrial vegetation (grasses and the like) as well as floating and rooted aquatic macrophytes whose roots, stems and leaves provide an important habitat for a wide range of animals. *Hydrilla verticillata* (Hydrocharitaceae), *Ludwigia adscendens* (Onagraceae), the duckweeds *Lemna minor* and *Spirodela polyrrhiza* (Lemnaceae), and water hyacinth, *Eichhornia crassipes* (Pontederiaceae), grew in profusion in lower Lam Tsuen before it was channelized. The submerged roots of water hyacinth, an exotic floating plant from South America, provided an important habitat for over 90 taxa of gastropods, odonate larvae, chironomid (Diptera) larvae, beetles and so on; many of these animals did not occur on or among the bottom sediments. The extent of macrophyte beds was, to a great extent, determined by the discharge volume of the river, and at times of high flow many of the plants were washed out to sea. During the dry season, by contrast, the river was almost choked by floating plants.

Spatial and temporal variations in benthic communities

It is not intended to give an exhaustive account of the longitudinal distribution of individual members of the benthic fauna of the Lam Tsuen River. Instead, discussion will be restricted largely to the zonation patterns of mayflies in order to give an indication of spatial and temporal patterns. Brief reference to caddisflies and snails will also be made for comparative purposes.

Thirty-one mayfly species have been recorded in an investigation of six sites along Lam Tsuen River. Twenty-one of these species were numerous and occurred at two or more sites; no mayflies were found among the bottom sediments at the lowest station, although they did occur among the roots of floating plants. Clear differences between families were apparent with respect to longitudinal zonation (Fig. 3). Baetidae were numerous at all sites where mayflies were found, but Caenidae were scarce upstream yet abundant further downstream. Many caenids inhabit silty substrata which are typical of the lower course of rivers; their distribution may reflect an adaptation of the morphology of the abdominal gills and the way that they beat. The beating of gills draws a current of water over the body of some mayflies, bringing it in from the front and sometimes the side also. Caenids have a reduced first gill, and the second forms an robust operculum overlying the abdomen and succeeding gills which are thin and delicate. When they beat, these gills cause a current from side-to-side across the body. If the animal rests on the substratum with one side slightly raised, it can draw water in from that side without disturbing the silt (HYNES 1970). *Caenis* larvae often inhabit deep sediments (the hyporheic zone) in river beds (WILLIAMS 1984), and light silting enhances their colonization of the interstices of coarse sediments (CUMMINS & LAUFF 1969). In these microhabitats the operculum may play a role in protecting the fragile gills from damage during burrowing.

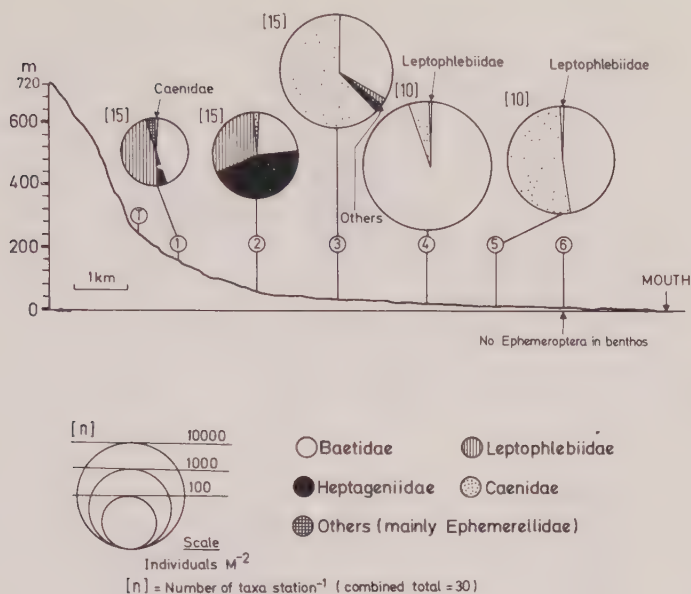


Fig. 3. The distribution and abundance of mayfly (Ephemeroptera) families along Lam Tsuen River during the wet season (summer 1978).

While there were inter-family differences in the longitudinal zonation of mayflies, divergence within families was also apparent. Among the Caenidae, *Caenis* tended to occur further down the river than *Caenodes* (Fig. 4), while the baetids *Indobaetis* and *Baetiella* characterized the two uppermost sites with *Baetis* T₃ and L₈ confined largely to the middle and lower course (Fig. 5). A few individuals of *Baetis* T₃ were present in the headwaters, but densities were low compared the abundance of this species downstream ($> 35000/\text{m}^2$ at Station 4). *Procloeon* L₁ was recorded at the lowest site supporting benthic mayflies; elsewhere in Lam Tsuen this insect was associated with trailing roots and grasses beside the river banks.

One explanation for interspecific variations in the zonation of baetids takes account of differences in respiratory adaptations. *Baetiella* inhabits turbulent headwater sites and has small, immobile abdominal gills which cannot beat to create a respiratory current; *Indobaetis* likewise relies on a strong flow of water to carry dissolved oxygen over the gills. Under conditions of respiratory stress *Baetis* spp. beat their gills to create a water current, while members of the lower-course genus *Procloeon* have moveable gills with expanded, lobed lamellae presenting a larger surface for gaseous exchange. *Cloeon* is found where the water is scarcely flowing (among weeds in lower Lam Tsuen River) or still; members of this genus have moveable gills with paired lamellae rather than the single, blade-like lamella that is typical of most Baetidae.

Whereas respiratory adaptations may be called upon to account for the longitudinal distribution of caenids and baetids, additional factors are important. Multiple regression analysis of mayfly population densities (dependent variables) on

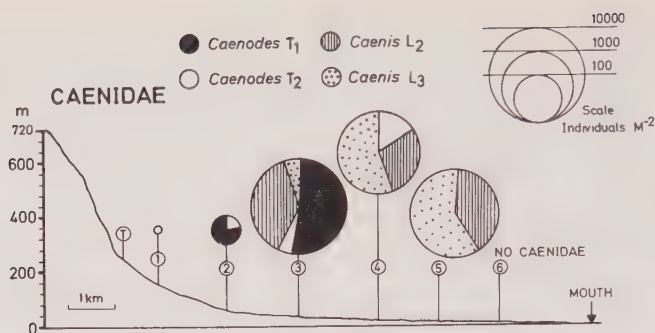


Fig. 4. The distribution and abundance of caenid mayflies (Ephemeroptera) along Lam Tsuen River during the wet season (summer 1978).

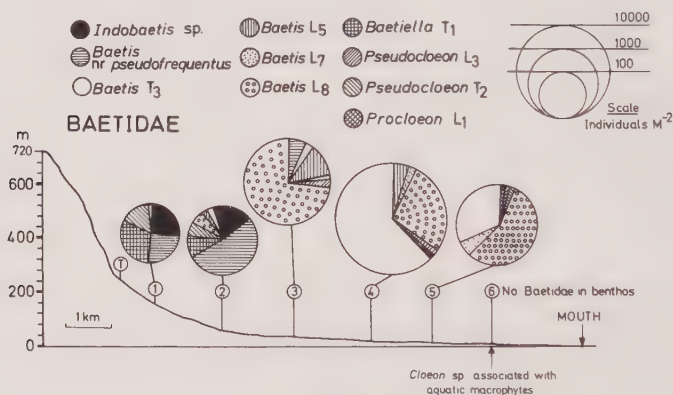


Fig. 5. The distribution and abundance of baetid mayflies (Ephemeroptera) along Lam Tsuen River during the wet season (summer 1978).

environmental parameters such as sediment characteristics and water chemistry (independent variables or predictors) show that the percentage of organic matter in the bottom sediments and the nitrite concentration of river water provide the best explanation for observed patterns of distribution and abundance (DUDGEON 1990a), although physical features of the sediments are sometimes important. There is interspecific variation in the response of baetids to these parameters (e.g. some species were abundant at sites with high levels of nitrite or sedimentary organics, other species avoided such localities), but taxa typical of the headwaters (*Baetiella* and *Indobaetis*) are not favoured by high nitrite levels. The same parameters are useful predictors of caenid abundance, with *Caenis* spp. responding positively to high levels of nitrites and sedimentary organics. The significance of nitrite loading as a predictor of mayfly abundance in the Lam Tsuen River gives a clear indication that zonation patterns in this habitat are influenced by organic pollution. Nitrite levels are low or undetectable in most streams unaffected by organic pollution, and

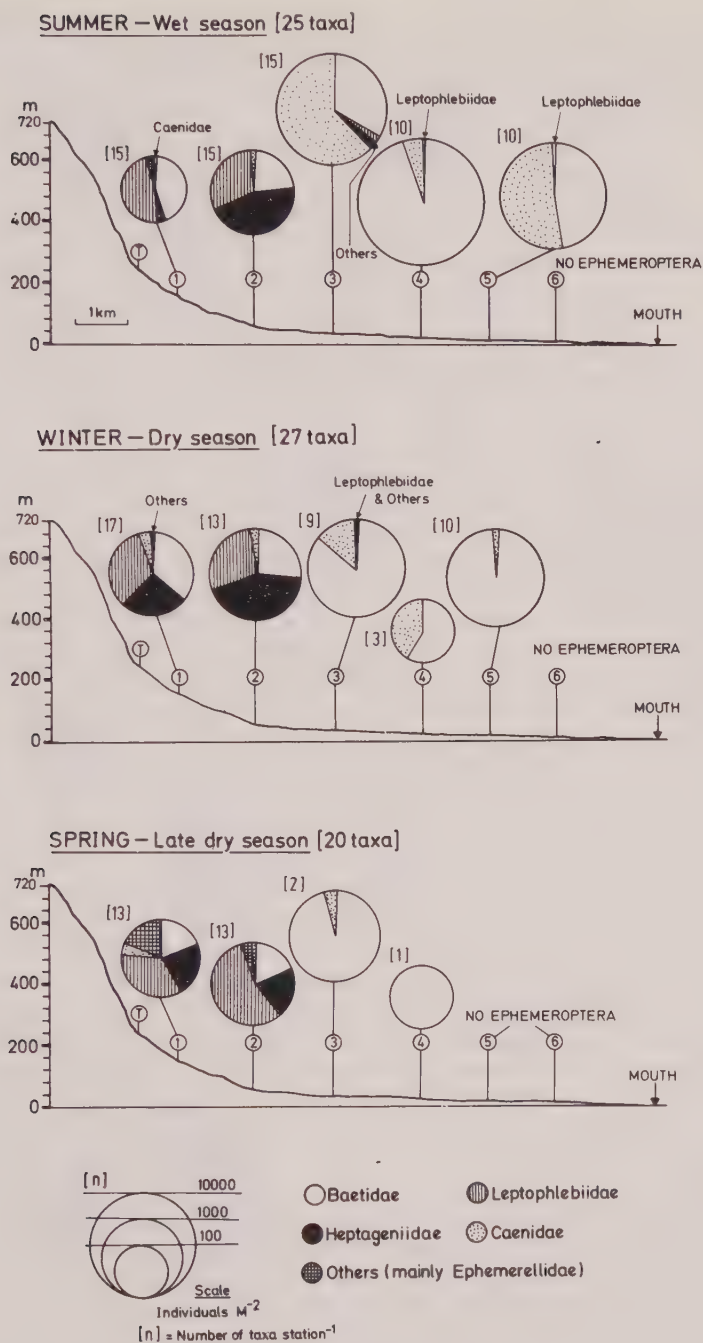


Fig. 6. Seasonal changes in the distribution and abundance of mayfly (Ephemeroptera) families along the Lam Tsuen River, 1978–79.

high concentrations in the lower course of the river indicate the presence of agricultural and domestic wastes (DUDGEON 1984a). Some of the increase in sedimentary organics in the lower course can be attributed to the same source.

Further evidence of the modification of natural zonation patterns by anthropogenic influences is apparent from seasonal changes in mayfly distribution and abundance over a year-long study (Fig. 6). During the wet season when river discharge volume was high, mayflies were found at stations 1–5, with three families present in the lower course, and one family (Heptageniidae) restricted to the two uppermost sites. During the winter dry season, lower discharge volumes led to an effective increase in organic pollution. The three downstream sites still supported baetids – the dominant family – and caenids, but leptophlebiid mayflies had been eliminated from Stations 4 and 5. By late spring when flows were lowest, mayflies could not be found at Station 5; caenids were no longer present at Station 4 and leptophlebiids (as well as other, less numerous families such as Ephemerellidae) had been ousted from Station 3 (Fig. 6).

The zonation of mayflies in Lam Tsuen River reflects the interaction of each species' match with the physical and chemical features of the local environment, and the modification of these habitat characteristics by seasonal changes in pollution load brought about by variations in river discharge volume. In essence, high flows during the wet season flush out the river so that the majority of its course is available for colonization by a variety of species. Greater pollution loads during the dry season eliminate many species from their preferred habitats and truncates mayfly distribution down the river. Recolonization of the lower course takes place after the onset of the summer monsoon and ensuing increases in river discharge.

A restriction of longitudinal zonation by pollution was also apparent among the benthic Trichoptera of Lam Tsuen River (DUDGEON 1984a, 1987a). Species richness declined downstream, and representatives of only two families (out of a total of seven for the whole river) were present in the lower course during the wet season (Fig. 7). By winter, only Hydropsychidae could be found at Stations 3, 4 and 5, although population densities of certain species increased in response to high food availability associated with organic pollution. As the dry season continued, caddisflies were eliminated from Stations 4 and 5, and the abundance of Hydropsychidae was reduced at Station 3. Only the two upstream sites supported a diverse trichopteran fauna throughout the year, and it is notable that two families – Rhyacophilidae and Glossosomatidae – were recorded only from the highest site. This pattern is in accordance with the altitudinal distribution of rhyacophilids and glossosomatids elsewhere in Asia and a requirement for cool, turbulent waters; indeed, these families have been referred to collectively as 'mountain caddisflies' (Ross 1956).

In contrast to the declines in certain benthic insects along the lower course of Lam Tsuen River, pulmonate snails colonized much of this region during the dry season (DUDGEON 1983a). In summer, pulmonates were abundant at Station 6 but were not recorded in benthic samples along the rest of the river. The prosobranch snail *Brodia hainanensis* (Thiaridae) was, by contrast, abundant in the upper course of Lam Tsuen, and is common in hill streams throughout Hong Kong (DUDGEON 1982b, 1989a). With the onset of the dry season, Stations 3–5 were invaded by pulmonates from drainage ditches and irrigation channels along the Lam Tsuen Valley. They comprised Planorbidae (*Hipppeutis cantonensis* and exotic *Biomphalaria*

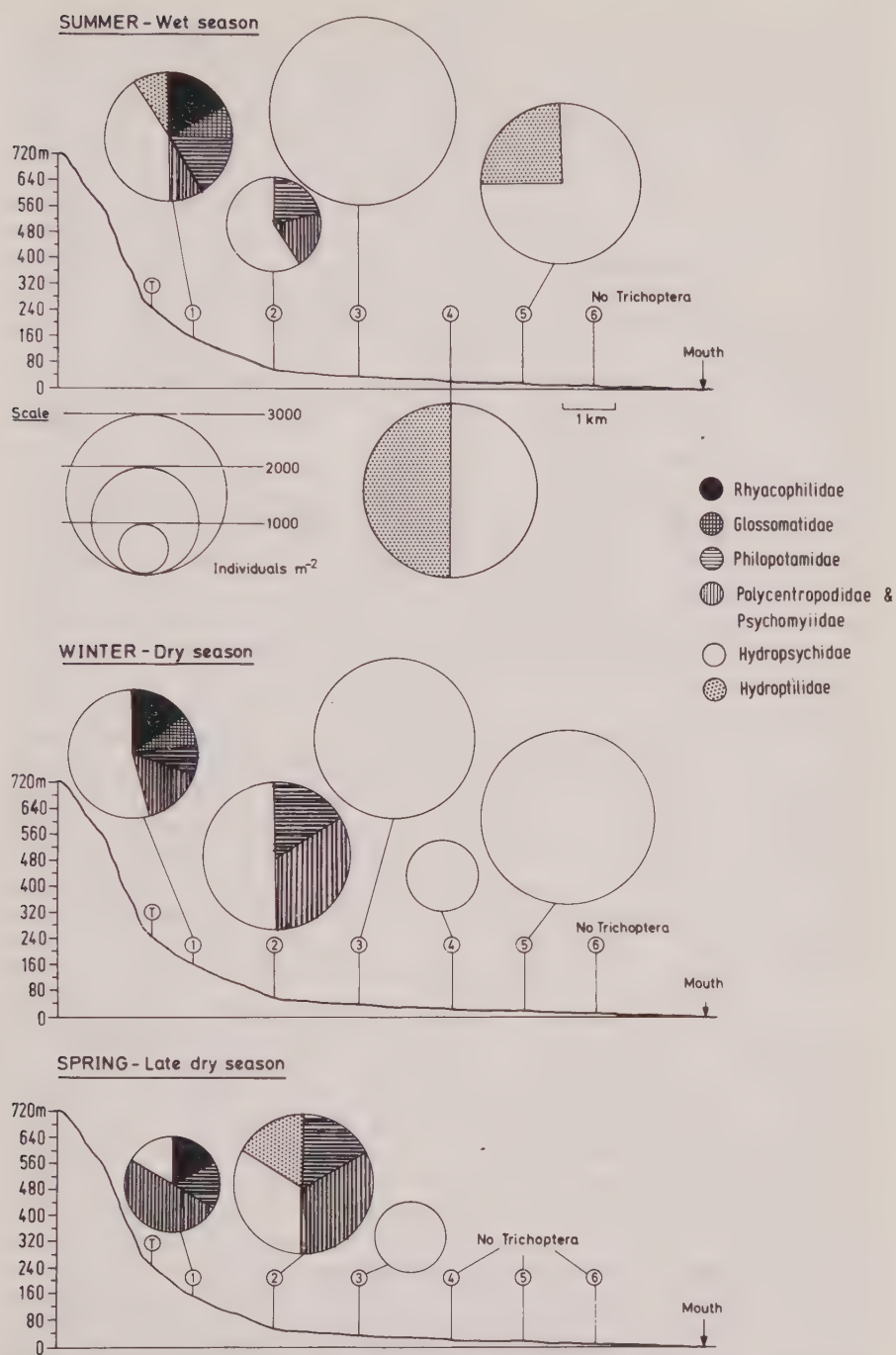


Fig. 7. Seasonal changes in the distribution and abundance of caddisfly (Trichoptera) families along the Lam Tsuen River, 1978-79.

straminea), Physidae (*Physella acuta*) and Lymnaeidae (*Radix auricularia plicatula*), families which exhibit some tolerance for organic pollution (HARMAN 1976). These snails were only able to establish themselves in the main river channel, and maintain position in the current, at times of low flow when organic enrichment was at its height. Under such circumstances, snail densities in excess of 2800/m² have been recorded.

In summary, the longitudinal zonation of benthic invertebrates in Lam Tsuen River is closest to that of a pristine water course during the wet season; increased organic loads as a consequence of decreasing flows in the dry season eliminate certain taxa from the lower course, but the greater food availability and lowered hydraulic stress in the river at this time favours the establishment of dense snail populations. Overall, the extent of the distribution of the natural community of the river is greatest in the wet season and least at the end of the dry season.

Functional organization of benthic communities

While some invertebrate families (e.g. baetid mayflies: Fig. 5) display a clear downstream replacement of species along the Lam Tsuen River, and other families are most numerous upstream (e.g. Heptageniidae) or in the lower course (e.g. Caenidae: Fig. 4), it is not clear whether the substitution of one taxon by another has any effect on community functioning. For example, the replacement of one species by another with a similar ecology may have negligible effect on processes such as the consumption and comminution of leaf litter. Alternatively, subtle changes in community composition and representation of individual species could result in major changes in community processes. To distinguish between these alternatives we can utilize the functional classification of animals according to similarities in resource utilization. Then, assuming that the River Continuum Concept provides a scale against which comparisons can be made (HAWKINS & SEDELL 1981; MINSHALL et al. 1983; NAIMAN et al. 1987), several problems can be addressed:

- 1) How do the general predictions of the River Continuum Concept apply to Lam Tsuen River?
- 2) How does the input of organic material and nutrients from agricultural and domestic sources affect benthic functional organization as predicted by the River Continuum Concept?
- 3) How are longitudinal patterns in functional organization influenced by seasonal fluctuations in river flow volume?

In summer, when flow volumes were high, the relative abundance of functional feeding groups approached that reported for northern temperate rivers. In particular, shredders were most abundant in the headwaters, filter-feeders increased in abundance downstream, and collector-gatherers were numerous along the entire river. Scraper populations were densest in the middle course and, as predicted, the relative abundance of predators along the river was fairly constant (Fig. 8). Collector-gatherers and filter-feeders were the most abundant groups at each station and, although shredders reached their highest densities in the headwaters (as predicted by the River Continuum Concept), they were the least numerous functional group at all sites where they occurred (DUDGEON, 1984b). The relative scarcity of shredders in the headwaters could be attributed to a lack of shading and

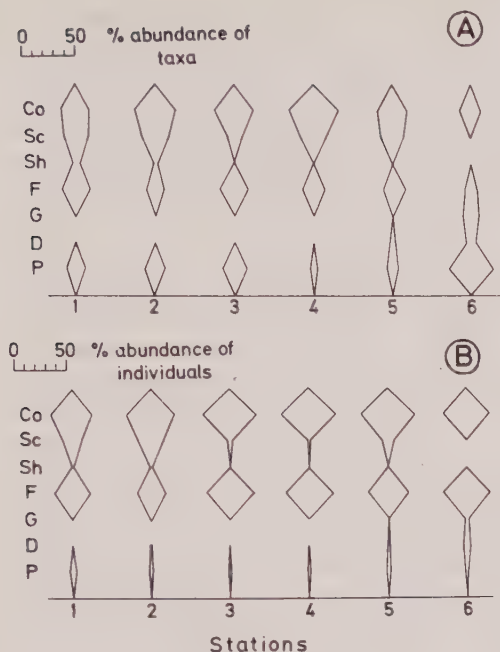


Fig. 8. The functional organization of macroinvertebrate communities at six stations along the Lam Tsuen River during the wet season (summer 1978) in terms of (A) the relative number of taxa comprising each functional feeding group, and (B), the proportionate abundance of each feeding group.

Abbr.: Co, collector-gatherers; Sc, scrapers; Sh, shredders; F, filter-feeders; G, generalists; D, deposit-feeders; P, predators.

limited allochthonous inputs from the surrounding landscape, much of which comprises shrubland. However, the upper tributaries of Lam Tsuen River flow through steep valleys where the riparian vegetation is secondary forest.

Functional group organization will differ from that predicted by the River Continuum Concept according to the riparian vegetation, substratum, and gradient of streams (HAWKINS *et al.* 1982), and local deviations from the general scheme can be expected (MINSHALL *et al.* 1983, 1985). Nevertheless, there is evidence that shredders are poorly represented in southern latitude streams (WINTERBOURN *et al.* 1981; LAKE *et al.* 1985; MARCHANT *et al.* 1985; BUNN 1986), and this may be typical of warm-temperate and tropical running waters.

Organic pollution of the Lam Tsuen River during the dry season altered the functional organization of the benthic community away from that predicted by the River Continuum Concept. Changes were confined to the middle and lower reaches of the river where generalists and deposit-feeders became locally abundant (Fig. 9B). These groups were relatively species-poor (Fig. 9A). Collector-gatherers and filter-feeders showed some increase in abundance relative to their densities during the wet season, but the increase was accompanied by a decline in the diversity of these groups in downstream reaches. Scraper and shredder distribution and diversity were also reduced by organic pollution. One indication of disruption of community structure was a decline in predator:prey ratios in the lower course of the river (Fig. 9C); this was due to a fall in predator densities which was particularly marked at the end of the dry season (DUDGEON 1984b). The increase in generalists, deposit-feeders, filter-feeders and collector-gatherers – as well as the decrease in taxa comprising the latter two groups in downstream reaches – reflected greater food

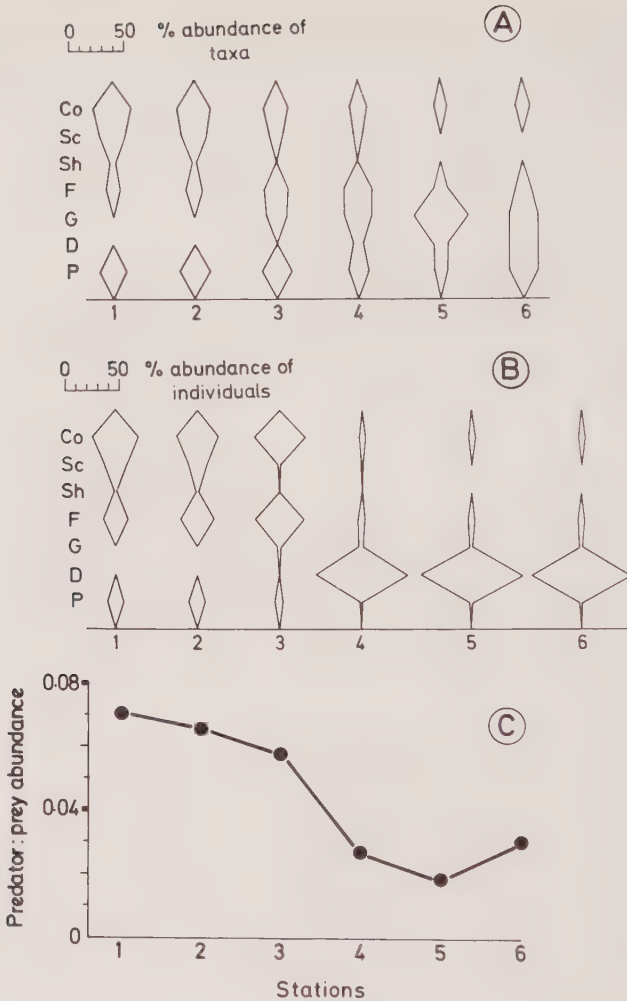


Fig. 9. The functional organization of macroinvertebrate communities at six stations along the Lam Tsuen River during the dry season (late winter 1979) in terms of (A) the relative number of taxa comprising each functional feeding group, and (B), the proportionate abundance of each feeding group. Longitudinal changes in the ratio of predator: prey abundance (1978–79) are also shown (C). Abbreviations as in Fig. 8.

availability in the polluted river. Some of this material accumulated in the bottom sediments, and high levels of organic matter were recorded from sediments where deposit-feeders abounded (DUDGEON 1984a).

In short, organic pollution of the lower reaches of the Lam Tsuen River simplified community structure during the dry season leading to a dominance of the benthos by deposit-feeders, and a large increase in the abundance of generalists. The summer monsoon flushed out the river with the result that filter-feeders and

(especially) collector-gatherers, which were numerous in the dry season, became the dominant functional groups at all sites; deposit-feeders and generalists were largely eliminated by the summer spates (DUDGEON 1984b). The functional organization of the two upstream sites, by contrast, did not change with season, indicating that alterations which occurred over the year at middle- and lower-course sites were a result of the interaction between rainfall seasonality and organic pollution rather than a consequence of season alone.

The stream and its valley

Leaving aside the effects of pollution, there was general agreement between longitudinal trends in the functional organization of Lam Tsuen River communities and those predicted by the River Continuum Concept. Those deviations which did arise, for example the scarcity of shredders, *may* be ascribed to local environmental vagaries (but see above), and there was an overall tendency towards gradual change in biotic conditions along the river. The local effects are nevertheless worthy of study as they can enhance our understanding of streams as components of higher landscape units. If we view the stream and its valley as an interacting unit (HYNES 1975), and assume that the aquatic community responds predictably to changes in the resource base (VANNOTE et al. 1980), then local variations in riparian vegetation should have a marked influence on in-stream processes. In other words, streams with similar physical characteristics and water chemistries will differ in their ecologies according to the vegetation of their valleys. To underscore the importance of the terrestrial influences upon streams, an account of research on Tai Po Kau Forest Stream will be given. This habitat is used as an illustration of the possible aboriginal conditions in Hong Kong running waters, because stream communities must have evolved in association with the forests which covered much of the earth's surface in primeval times. The account will then be expanded to present a comparison of the effects of riparian vegetation on the ecology of Hong Kong hillstreams.

Tai Po Kau Forest Stream

General characteristics: the abiotic environment

Tai Po Kau Forest is a managed nature reserve on the southwestern shores of Tolo Harbour (Fig. 1). Although the vegetation includes introduced species and secondary forest, the majority of plants are native to South China and to this extent the reserve represents conditions prevailing on Hong Kong hillsides prior to forest clearance. The reserve is drained by 3.6 km-long Tai Po Kau Forest Stream which rises 400 m above sea level; the forested area of catchment is approximately 2.5 km². This drainage basin is composed predominately of pyroclastic rocks with intrusions of lava, and can be characterized as Repulse Bay Formation (ALLEN & STEPHENS 1971). The soils are lateritic krasnozems with a pH of around 5, and the rocks in and around the stream bed comprise an undifferentiated colluvium of boulders with finer interstitial material.

Table 3. Tai Po Kau Forest Stream: hydrological features.

Water temperature	– 11.3–26.7 °C (1977–78), 15.5–26.0 °C (1978–79), 14.5–25.8 °C (1983–84)
pH	– 6.8 (range 6.5–7.0)
Silica	– 17.8 ± 5.3 mg/l
Alkalinity	– insignificant
Total hardness	– < 2.0 mg/l
Chloride	– 12 mg/l
Iron	– 0.1 mg/l
Dissolved oxygen	– > 7.7 mg/l
Phosphate	– < 0.1 mg/l; fluctuations associated with spates
Nitrate	– 0.03 mg/l (up to 0.16 mg/l)
Nitrite	– generally < 0.01 mg/l (range 0–0.06 mg/l)
BOD _{5-day}	– 0.05 mg/l No seasonal trends
BOD _{24-day}	– 1.4 mg/l
Seston	– generally 2 mg/l but up to 55 mg/l during spates; generally > 60 % organic matter

Tai Po Kau Forest Stream waters are poor in dissolved minerals and slightly acidic (Table 3). B.O.D. and seston loads are seasonally variable and influenced by the timing and extent of allochthonous leaf-litter inputs (DUDGEON 1982a). Much of the physical environment of the stream reflects the transport and deposition of inorganic particles by the current. The stream bed is composed of boulders with rocks and gravel forming the substrate between them; sand occurs in isolated pockets sheltered from the current along the stream margins and under, or in the lee of, large rocks and boulders. In general, the stream sediments are coarse grained, poorly sorted and leptokurtic (DUDGEON 1982c), with a positive skew towards a predominance of large particles. Substrate characteristics change across the stream bed, with increasing proportions of fine particles and greater sorting in sediment patches close to the banks (Fig. 10).

Inter-patch differences in sediment characteristics promote environmental heterogeneity within the stream, and have important implications for the micro-distribution of benthic invertebrates (DUDGEON 1982c, 1982d, 1990a). Spates associated with summer monsoonal rains scour the stream bed and wash fine particles downstream. Inter-patch heterogeneity is thereby reduced, with the result that bankside and midstream sediments become similar. Across-stream gradients in particle size and substrate characteristics are reestablished as discharge volumes decline and stabilize during autumn and winter, and sediment heterogeneity is restored (DUDGEON 1982c).

Implicit in the across-stream sediment gradients are the effects of current velocity. Direct measurements have shown that, as expected, current velocities are highest in midstream sites (> 50 cm/sec) and lowest close to the banks (generally < 10 cm/sec). Boundary layer effects are prominent (due to the resistance to water flow caused by the friction of the stream bed), and current velocities decrease markedly with proximity to the bottom sediments (DUDGEON 1982c); dead water spaces are evident downstream of obstructions to flow. Note that these rather static films and pockets of water are important microhabitats for benthic organisms, and

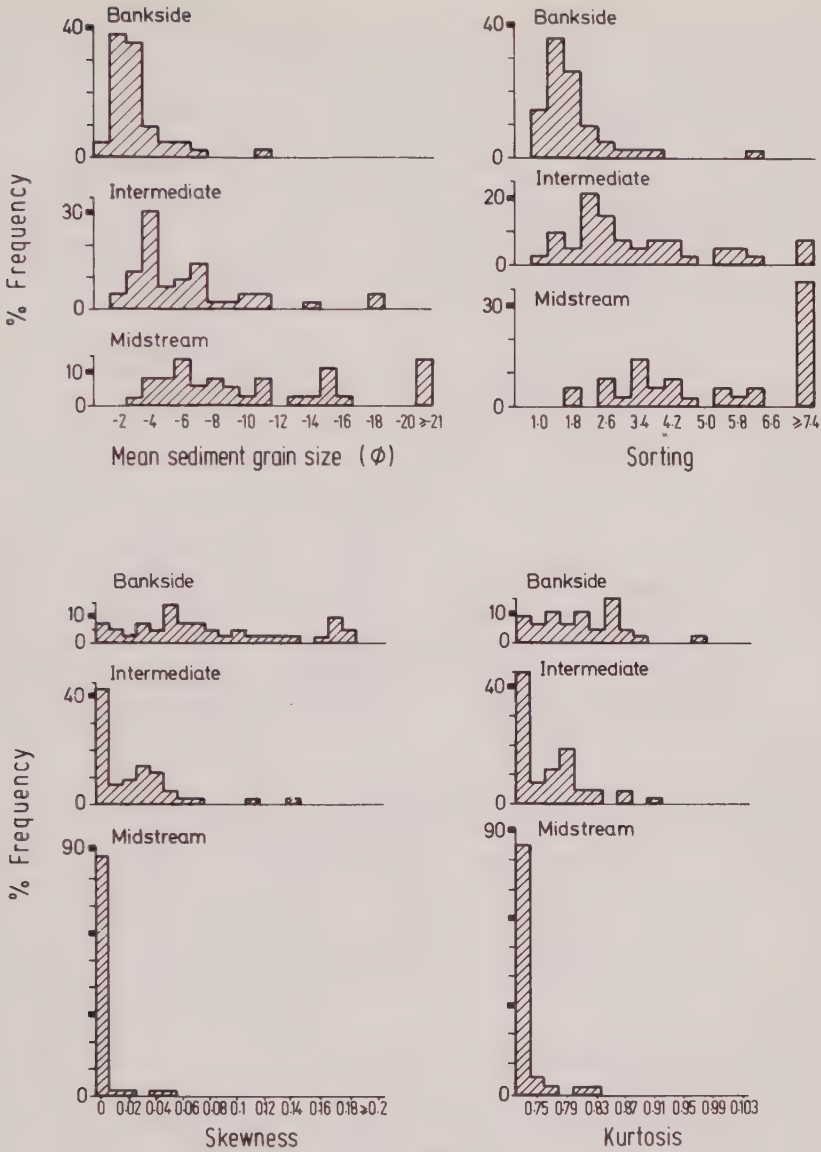


Fig. 10. Changes in sediment characteristics across a riffle reach of Tai Po Kau Forest Stream, based on analyses of samples collected at bankside, midstream and intermediate microsites over a two-year period. Particle size is expressed in phi units ($= -\log_2$ particle size in mm).

provide a refuge from the full force of the current. Accordingly, most stream fauna have morphological or behavioural adaptations for life in the boundary layer or in areas of dead water (see part III). As a result, microdistribution patterns are not determined as much by the direct effects of current as by the effects of water flow on the transport and deposition of inorganic particles; i.e. substratum characteristics are the major factor controlling the occurrence of animals (HYNES 1970). The boundary layer does, of course, become thinner with faster rates of flow, and it is not possible for the benthos to escape entirely from the effects of current. Indeed, hydraulic variables do play an important role in the metabolism, feeding, and behaviour of lotic organisms, and we still have much to learn about the complex effects of stream flow on the benthos (STATZNER et al. 1988).

Microdistribution of benthic animals

The significance of the physical environment in determining the microdistribution of benthic insects in Tai Po Kau Forest Stream is apparent from the patterns of abundance of individual species across the stream (DUDGEON 1982d). Population densities change in parallel with across-stream variations in sediment characteristics, and different taxa, as well as individual species within the same family, display distinctive distribution patterns (DUDGEON 1982d, 1990a). For example, among the mayflies, four common Baetidae show three distinct types of distribution pattern (Fig. 11), with population densities peaking at midstream (*Baetis* nr *pseudofrequentus*), bankside (*Chopralla* sp.) or intermediate (*Baetis* T₃) sites; the across-stream microdistribution of *Indobaetis* sp. resembles that of *Baetis* nr *pseudofrequentus*. Contrasting microdistribution patterns are also seen among leptophlebiids: *Thraulius* cf. *bishopi* and *Habrophlebiodes gilliesi* are most numerous close to the stream banks, while *Isonia purpurea* densities peak in midstream (Fig. 12).

Regression analysis of population densities of individual mayfly species against a range of environmental parameters including sediment statistics (mean grain size, sorting, skewness and kurtosis), sedimentary organic matter, as well as detrital and algal standing stocks, indicate that the primary factor determining the microdistribution of all but one (*Baetis* T₃) of these mayflies is sediment characteristics (DUDGEON 1990a). Algal and detrital standing stocks serve as additional statistically-significant predictors for three species, but are valuable only when used in association with sediment statistics. Similar investigations on dragonfly and damselfly larvae in Tai Po Kau Forest Stream over a two-year period have confirmed the importance of organism-substrate interactions as determinants of microdistribution, three out of four species favouring poorly-sorted sediments with highly-peaked grain-size distributions containing few fine particles (DUDGEON 1989b, 1989c). Laboratory investigations have also revealed marked preferences for particular substrate types by four benthic fish species from Tai Po Kau Forest Stream (DUDGEON 1987b).

It seems clear that sediment characteristics are important determinants of the microdistribution of benthic animals within a particular stream reach. By contrast, the distribution of species along the Lam Tsuen River is determined by water quality or the amount of organic material in the sediments rather than by the physical nature of the substratum. This difference reflects sampling scale. Collections at each site along the Lam Tsuen River were made from relatively large

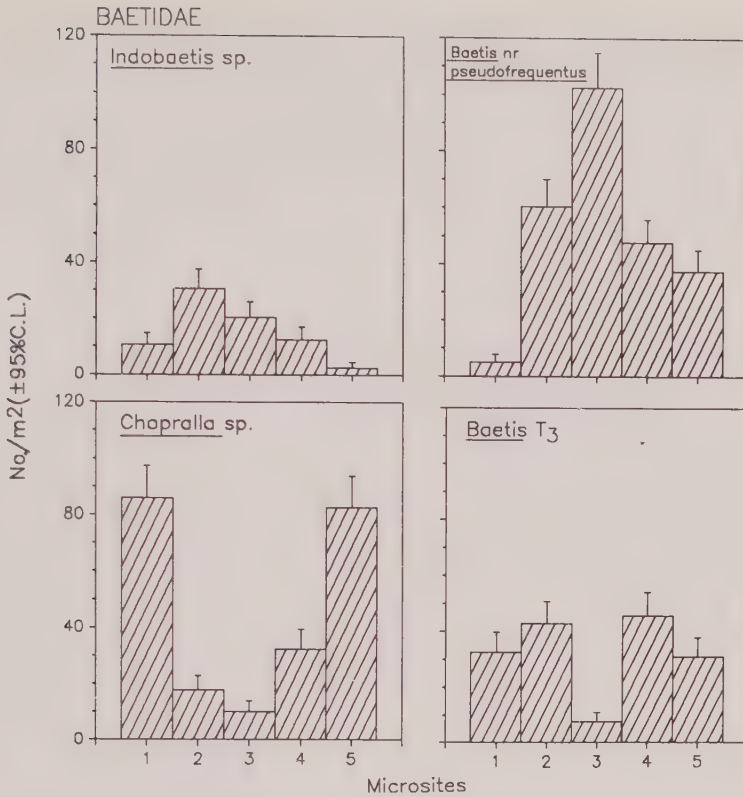


Fig. 11. The abundance of baetid mayflies (Ephemeroptera) across the width of Tai Po Kau Forest Stream, where microsites 1 & 5 were close to the banks, microsite 3 was midstream, and 2 & 4 were in intermediate positions.

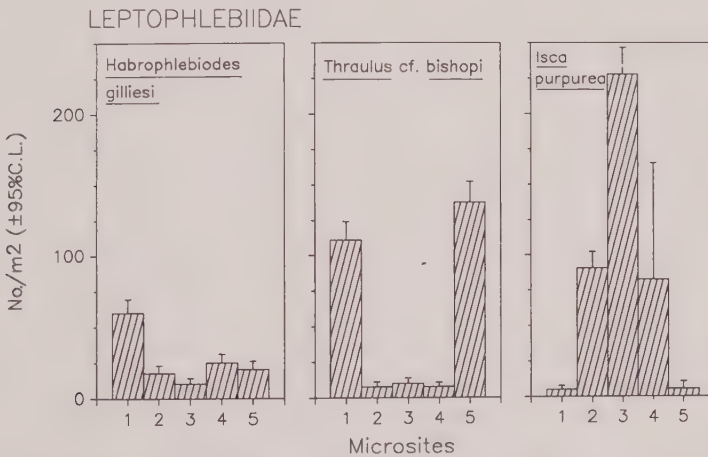


Fig. 12. The abundance of leptophlebiid mayflies (Ephemeroptera) across the width of Tai Po Kau Forest Stream, where microsites 1 & 5 were close to the banks, microsite 3 was midstream, and 2 & 4 were in intermediate positions.

areas incorporating a high degree of substratum heterogeneity, but the Tai Po Kau samples were taken from smaller areas with limited heterogeneity within each sampling unit. Nevertheless, the conclusion that microdistribution is determined largely by substratum characteristics (and so indirectly by current) remains valid, with both particle size and sediment heterogeneity (sortedness, skewness and kurtosis) comprising important components of the habitat template. These findings are in agreement with research on temperate stream invertebrates (CUMMINS & LAUFF 1969; HYNES 1970; MINSHALL & MINSHALL 1977; MINSHALL 1984).

General characteristics: the biotic environment

The biological environment of Tai Po Kau Forest Stream is influenced profoundly by riparian trees which cast shade, reducing the intensity of light reaching the water surface. As a result, periphyton standing stocks are low, although thallose *Rivularia* (Cyanophyta or blue-green bacterium) is locally common and the red alga *Batrachospermum* (Rhodophyta) may be encountered at shaded sites sheltered from the current. Areas closest to the stream banks, where slow flows and reduced scour permit algae to accumulate, have the highest standing stocks of periphyton (DUDGEON 1982e). There is evidence that Chlorophyta (unicellular and filamentous green algae) are more abundant close to the banks, while higher proportions of diatoms (Bacillariophyta) occur in midstream. Spates cause substantial reductions in periphyton standing stocks, and a wet-season decline of $323.4 - 21.8 \text{ mg/m}^2$ was recorded during a two week-period in August marked by a major spate; a further decrease to 9.6 mg/m^2 was apparent over the following two weeks (DUDGEON 1982e). There is thus marked temporal variability in the availability of autochthonous food sources to stream consumers. There are no aquatic macrophytes in Tai Po Kau Forest Stream although bryophytes (largely mosses) and lichens (*Verrucaria* sp.: Verrucariaceae) encrust boulders and tree roots just above the water level.

Apart from the influence exerted by riparian vegetation shading the stream bed, trees contribute allochthonous detritus in the form of fallen leaves, twigs, and branches. These form conspicuous accumulations in areas of slow flow, and constitute dense packs in places where water is funnelled between large boulders. Standing stocks of allochthonous detritus in Tai Po Kau Forest Stream are always high (dry weight $> 40 \text{ g/m}^2$) and exceed periphyton biomass by over 100 times (DUDGEON 1982c). There are rather small spatial and seasonal variations in the amounts of detritus in the stream, although a minor increase in standing stocks close to the banks from December to February reflects litter input from deciduous *Liquidambar formosana* (Hamamelidaceae) which is common along some reaches. This winter input is probably not typical of Tai Po Kau Forest Stream as a whole, nor Hong Kong streams in general, since leaf-fall in Hong Kong peaks during spring and early summer (March - July), and rates of leaf-fall are positively correlated with prevailing temperature and rainfall (LAM & DUDGEON 1985). Direct leaf-fall (from the overhanging closed canopy) into Tai Po Kau Forest Stream exceeds $750 \text{ g (dry weight)/m}^2/\text{yr}$, in addition to over $370 \text{ g (dry weight)/m}$ stream bank/yr carried in by lateral transport (DUDGEON 1982e). Elsewhere in Hong Kong, an annual litter-fall of $1219 \text{ g (dry weight)/m}^2$ (comprising 69% leaves) has been recorded, but typhoons have an important effect on the magnitude and timing of litter production (LAM & DUDGEON 1985).

Although there is some variation between species, terrestrial leaves are broken down rapidly in Tai Po Kau Forest Stream, with complete disappearance occurring in less than 13 weeks (DUDGEON 1982f). Sedimentary organic matter, derived largely from the breakdown of allochthonous litter, shows spatial variations related to its incidence in different substrate particle-size fractions, fine grains having a high percentage of organic material (DUDGEON, 1982c). Consequently, the quantities of sedimentary organics correlate with the distribution of fine inorganic particles, and the stream bed close to the banks contains the largest amounts of organic matter. Declines in the fine-particle fraction of the substratum during spates are accompanied by a fall in sedimentary organics (DUDGEON 1982c).

Despite high standing stocks of allochthonous detritus in Tai Po Kau Forest Stream, there is no association between mayfly microdistribution patterns and detrital standing stocks or the amounts of sedimentary organics (see above; DUDGEON 1990a). By contrast, periphyton biomass is a predictor of abundance for certain species. While these data may reflect the importance of algae in determining the abundance of a few specialized herbivores, they cannot be interpreted as an indication that detritus plays no role in governing microdistribution patterns. Detrital standing stocks exceed periphyton biomass by over 100 times, and it is likely that all patches are well-endowed with detrital food; only if detritus is limiting would we expect it to influence mayfly microdistribution, and a lack of association would be expected if the amounts were in excess of requirements (MINSHALL & MINSHALL 1977; PECKARSKY 1980; DUDGEON 1990a).

The trophic basis of production

In view of the large standing stocks of allochthonous detritus and rapid leaf-litter processing in Tai Po Kau Forest Stream, it could be supposed that autochthonous primary production plays a minor role in the nutrition of benthic animals. This supposition is only reasonable, however, if the algae and detritus have equivalent food value. There is reason to believe that this is not the case, and substantially different assimilation efficiencies have been derived for lotic invertebrates feeding on algal cells and detritus (BENKE & WALLACE 1980). Much allochthonous detritus comprises structural polysaccharides (cellulose, hemicellulose and lignin) which are not readily digested by most aquatic insects (MARTIN et al. 1981, MATTINGLY 1987a), requiring colonization by microbes to make them palatable to consumers (McLACHLAN 1978; ANDERSON & SEDELL 1979; CUMMINS & KLUG 1979; BÄRLOCHER 1985). Differences in nutrient content, tannin levels and leaf toughness among types of litter, as well as the species composition of colonizing microbes, will affect their consumption by invertebrates (IRONS et al. 1988; PEARSON & TOBIN 1989; ARSUFFI & SUBERKROPP 1989). Inadequate characterization and/or quantification of potential food supply may, therefore, lead to ambiguous relationships between consumer densities and detrital standing stocks (HAWKINS & SEDELL 1981). By contrast, algal cells comprise a greater proportion of readily-assimilable material (THOMPSON 1987) and therefore constitute a valuable food (BIRD & KAUSHIK 1984; ROSILLON 1988), although not all algae are similar in nutritional quality (FULLER et al. 1988), digestibility (THOMPSON 1987) or the ease with which they can be removed from the substratum and ingested (PETERSON 1987). Moreover, a simple measure of periphyton biomass may underestimate the importance of

this food if the algal cells have a fast turnover. Additional difficulties will arise if invertebrates require mixed diets, and there is evidence that mayflies which ingest algae and detritus in nature will grow at different rates on pure diets of one or other food type (WEBB & MERRITT 1987; ROSILLON 1988).

A more realistic measure of the relative importance of allochthonous and autochthonous food sources can be obtained by evaluating the amount of energy fixed by in-stream photosynthesis per unit time, and the amount of energy respired by the stream community over the same time. Any shortfall in energy demand must be made up from allochthonous sources. Measurements of community respiration (R) and primary production (P) in a shaded reach have yielded a P/R ratio of 0.17 (Table 4), confirming the stream's dependence upon allochthonous energy sources (DUDGEON 1983b). Indeed, a heterotrophic community metabolism is a common feature of forest streams in temperate latitudes (HALL 1972; FISHER & LIKENS 1973; CUMMINS 1974; but see ROSENFELD & MACKAY 1987 and MEYER 1989). Furthermore, in an unshaded pool of Tai Po Kau Forest Stream, containing abundant periphyton, a P/R ratio of 1.02 was recorded (Table 4); even at well-lit sites, community respiration almost exceeds primary production (DUDGEON 1983b).

Table 4. Tai Po Kau Forest Stream: primary production and community respiration.

	Mean current speed (m/sec)	Temperature range	Exchange coefficient ($f_{20^\circ\text{C}}$)
Pool site	0.12 ± 0.02	21–22.8°C	13.2 cm hr ⁻¹
Riffle site	0.71 ± 0.07	21–22.8°C	16.73 cm hr ⁻¹
	Primary productivity, P (mg O ₂ /m ² /day)	Community respiration, R (mg O ₂ /m ² /day)	$P : R$
Pool site	67.36	66.24	1.02
Riffle site	27.63	159.05	0.17

Methods following the twin-curve dissolved oxygen technique (OWENS 1974).

Riparian vegetation and stream communities

Community composition

The basis of the River Continuum Concept is that invertebrate communities are dynamically linked to energy sources and structured predictably to utilize their energy income most efficiently (VANNOTE et al. 1980). The Concept therefore provides a theoretical framework within which the results of studies focusing on the trophic basis of production (allochthonous versus autochthonous) can be contained. In addition to the expected longitudinal changes in the food base of running waters, local influences may lead to differences in the ecology of streams of

equivalent size which are situated in separate drainage basins. Riparian vegetation can have marked effects on the community structure of North American streams (HAWKINS *et al.* 1982, 1983), and experimental manipulation of the extent of shading (TOWNS 1981; FULLER *et al.* 1986), as well as removal of the riparian canopy by logging (WALLACE & GURTZ 1986), have demonstrated the importance of changes in the relative proportions of autochthonous and allochthonous energy sources.

The ecology of Tai Po Kau Forest Stream is dominated by allochthonous influences, but we would expect a change in community structure across a gradient of decreased shading by riparian vegetation. It has been possible to identify four, similar-sized Hong Kong streams, including Tai Po Kau Forest Stream, which differ with respect to shading and consequently show inter-site variations in detrital inputs and periphyton standing stocks. These streams provide the opportunity for a natural 'snapshot' experiment (*sensu* DIAMOND 1986) on the interaction between lotic macroinvertebrate communities and their food.

The study sites were riffle reaches of streams in separate watersheds; three are situated in central New Territories, with a fourth on Lantau Island (Fig. 13). The streams were similar with respect to width, depth, current speed and bottom sediments. All were unpolluted and showed no major differences in water chemistry (DUDGEON 1988a). The Tai Po Kau Forest Stream study riffle was entirely shaded by riparian trees with canopies interlocking over the stream; Bride's Pool was also surrounded by trees but their canopies did not shade the entire stream bed. Riparian

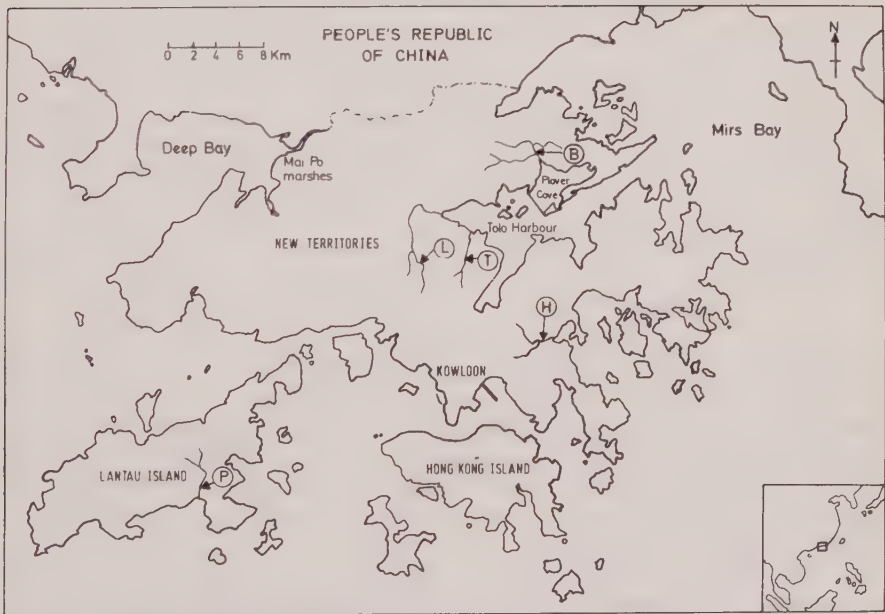


Fig. 13. A map of Hong Kong showing the locations of Pui O Stream (P; Lantau Island), as well as the Lam Tsuen River (L), Tai Po Kau Forest Stream (T), Bride's Pool (B), and Ho Chung River (H; New Territories). These habitats have been the main sites of investigations undertaken on Hong Kong's lotic biota.

vegetation along an upper tributary of the Lam Tsuen River site comprised scrub and tall grasses with few trees, and the stream was almost completely exposed to the sunlight. Pui O Stream was unshaded and the riparian grassland vegetation was of low stature; dense growths of periphyton reflected the amount of light reaching the stream bed.

Intersite variations in the degree of shading affected standing stocks of allochthonous detritus, which were significantly higher in Bride's Pool and Tai Po Kau Forest Stream than elsewhere. (Table 5). Periphyton biomass also differed significantly and was greatest at the unshaded sites, attaining a maximum in Pui O Stream; both Tai Po Kau Forest Stream and Bride's Pool supported sparse algal growths. A clear distinction could be made between shaded streams, exhibiting an apparent allochthonous food base, and streams with an open canopy which had lower detrital standing stocks and greater autochthonous resources. Community composition varied considerably among streams and only 27% of the total of 126 taxa collected occurred at all four sites. Tai Po Kau Forest Stream supported the lowest densities of benthic macroinvertebrates but the greatest variety of taxa (94 out of a combined total of 126); species relative abundance was also more even and few taxa were numerous (i.e. most species were rare). Differences in total macroinvertebrate abundance across sites could not be directly related to periphyton or detritus standing stocks (DUDGEON 1988a), and there was no relationship between the total number of animals and algal or detrital biomass in each sample.

Table 5. Inter-site differences in detrital and algal standing stocks (mean \pm 1 S.E.M.) among four Hong Kong streams.

	Tai Po Kau Forest stream (T)	Bride's Pool (B)	Lam Tsuen River (L)	Pui O stream (P)	Site rankings
Detritus (g/m ²)	66.0 \pm 22.6	39.3 \pm 7.6	10.8 \pm 2.3	16.8 \pm 3.9	T, B > L > P
Total chloro- phyll (mg/m ²)	6.3 \pm 1.1	4.1 \pm 1.5	17.7 \pm 8.1	64.4 \pm 8.1	P > L > T, B

Examination of the 12 most abundant species from each stream (comprising 30 species in total) showed that only two were common to all sites, and 17 were numerous in only one of the four streams (Table 6). The species composition and the densities of the most numerous taxa were rather similar in Tai Po Kau Forest Stream and Bride's Pool, and also in Lam Tsuen River and Pui O stream, but were generally different between the two pairs of sites. In other words, the benthic communities of shaded streams were different from those of unshaded streams. The importance of algae and detritus as determinants of abundance of individual species was emphasized by regression analysis which yielded significant explanation of inter-stream differences in the population densities of two-thirds of the 30 most numerous species. Thus standing stocks of algae or detritus (and sometimes a combination thereof) could be used to predict the abundance of the majority of the commoner invertebrates among the four streams. By contrast, the abundance of

Table 6. The abundance (Mean no./0.1 m² ± 1 S.E. M.) of the 12 top-ranked taxa from four Hong Kong streams. The number of taxa (= morphospecies) and the proportion of the total benthos comprising top-ranked taxa in each stream are also shown.

Tai Po Kau Forest Stream	Bride's Pool	Lam Tsuen River	Pui O Stream
<i>Chimarra</i> T ₁	25.8 ± 7.2	185.8 ± 61.0	<i>Baetis</i> nr <i>pseudofrequentus</i>
<i>Cheumatopsyche</i> cf. <i>spinosa</i>	17.7 ± 5.0	83.3 ± 31.0	<i>Cheumatopsyche</i> L ₄
<i>Serratella</i> T ₂	13.2 ± 3.0	45.3 ± 6.4	<i>Baetis</i> nr <i>pseudofrequentus</i>
<i>Simulium</i> T ₁	12.7 ± 9.8	29.4 ± 10.8	<i>Pseudocloeon</i> T ₂
<i>Choroterpes</i> spp.	11.9 ± 5.5	27.6 ± 22.0	<i>Zygonyx iris</i>
<i>Cheumatopsyche</i> TdB	11.7 ± 2.5	24.9 ± 17.6	<i>Choroterpes</i> spp.
<i>Indobaetis</i> sp.	8.4 ± 2.8	18.4 ± 6.6	<i>Pseudocloeon</i> L ₃
<i>Pseudocloeon</i> T ₂	8.4 ± 2.8	14.6 ± 5.5	<i>Baetis</i> T ₃
Elmidae larva #4	7.8 ± 2.6	10.0 ± 2.3	<i>Enochrus</i> sp.
<i>Herbertosia quadrata</i>	7.2 ± 3.2	9.5 ± 8.6	<i>Caenodes</i> T ₁
<i>Eubrianax</i> sp.	5.6 ± 1.2	7.6 ± 2.1	Elmidae larva #2
<i>Eulichas</i> sp.	5.1 ± 4.8	7.1 ± 2.1	<i>Hydropsyche chekiangana</i>
Total population density	240.8 ± 39.8	548.2 ± 128.9	<i>Cheumatopsyche</i> Lz
% total comprising top-ranked taxa	56.3	84.5	9.4 ± 9.3
No. morphospecies	94	80	455.5 ± 63.8
		86	84.4
			79.4
			70

taxa within a particular stream could only be predicted by regression models including algae or detritus in three out of 30 cases (DUDGEON 1988a). Clearly, inter-stream differences in the abundance of individual species were a consequence of the amounts of allochthonous or autochthonous food but, with a few exceptions, microdistribution in individual streams could not be ascribed to inter-patch differences in the amounts of algal or detrital food. As data derived from studies of Tai Po Kau Forest Stream have demonstrated (see above and DUDGEON 1990a), microdistribution patterns seem generally to reflect substrate heterogeneity rather than food availability (but see BARMUTA 1990).

Riparian vegetation has a marked influence on the community composition of benthic animals in Hong Kong streams. Components of the benthos show species-specific responses to standing crops of algae and detritus, such responses apparently causing inter-stream differences in community composition. These data provide support for the River Continuum Concept in that Hong Kong stream animals respond predictably to changes in the relative contributions of allochthonous and autochthonous energy sources. Nevertheless, a necessary corollary of the River Continuum Concept is division of stream animals into functional feeding groups. Complete understanding of differences in community composition requires such division in order to yield information on functional organization. These data are essential, because replacement of species by ecological equivalents may not result in any change in trophic structure within the stream system.

Functional organization

Population densities of all functional groups except predators differed significantly between the four streams (Table 7). As predicted by the River Continuum Concept, scrapers were most abundant at the unshaded sites, while shredders were most numerous in Tai Po Kau Forest Stream which had the highest standing stocks of detritus (DUDGEON 1989d). Shredders were also proportionately more abundant in Tai Po Kau Forest Stream (Fig. 14), but the relative abundance of scrapers did not change between sites. The high densities of scrapers in unshaded Pui O Stream and Lam Tsuen River reflected relatively high total population densities rather than a change in the proportional representation of functional groups (Fig. 14). Pierceers

Table 7. Inter-site differences in functional group abundance (mean no./0.1 m² ± 1 S.E.M.) among four Hong Kong streams.

	Tai Po Kau Forest Stream	Bride's Pool	Lam Tsuen River	Pui O Stream
Predators	26.4 ± 4.0	69.4 ± 36.3	48.3 ± 16.4	20.2 ± 3.7 *
Scrapers	38.8 ± 5.1	59.3 ± 8.1	113.0 ± 12.8	96.5 ± 14.8*
Collector-gatherers	74.2 ± 10.4	312.7 ± 74.8	257.9 ± 28.7	202.8 ± 35.9*
Filter-feeders	83.3 ± 25.3	104.4 ± 31.1	215.4 ± 50.2	87.1 ± 14.1*
Shredders	19.9 ± 3.4	4.9 ± 1.0	6.9 ± 1.6	0.5 ± 0.3*
Pierceers	0	0	0.1 ± 0.1	8.1 ± 2.4*
Total population	240.8 ± 39.3	548.8 ± 128.9	665.8 ± 101.9	445.5 ± 63.8*

* = significant ($P < 0.05$) inter-stream difference

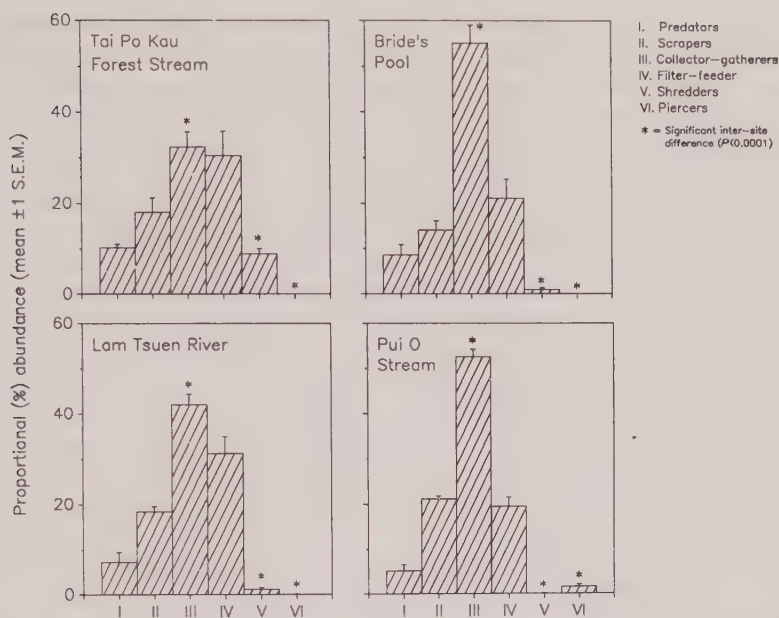


Fig. 14. Differences in the proportional abundance of macroinvertebrate functional feeding groups among four Hong Kong streams.

and suckers of plant cells (hydroptilid caddisflies) attained highest densities and relative abundance at Pui O Stream, a result of the dense growths of filamentous algae at that site.

Regression analysis showed that the relative and absolute abundance of shredders could be explained by a combined model that included a positive association with detritus and a negative association with algae (DUDGEON 1989d). Piercer abundance was determined by periphyton, while scraper densities (and proportional representation) were strongly negatively related to detrital standing stocks; this may represent an indirect effect of shading on periphyton rather than a deleterious influence of detritus *per se* (DUDGEON 1989d). Collector-gatherers were weakly associated with detrital standing stocks, and neither the abundance of predators nor filter-feeders could be significantly predicted by any regression model including the biomass of algae and/or detritus. Predator abundance was, however, strongly related to the densities of collector-gatherers plus filter-feeders, the most numerous groups of potential prey. Filter-feeder densities were determined by the combined abundance of collector-gatherers, shredders and scrapers (DUDGEON 1989d) and, through their feeding activities (comminution of coarse detritus, production of faecal pellets, and dislodgment of periphyton), these animals may have produced suspended particles suitable for ingestion by filter-feeders.

Overall, changes in functional group representation showed some agreement with the River Continuum Concept. There was evidence of the role of algae and detritus in determining the relative abundance and/or population densities of certain groups, while predator abundance was related to the combined densities of

prey. Nonetheless, the representation of collector-gatherers and filter-feeders (together comprising the most abundant functional groups and the majority of the fauna at each site) was not clearly related to trophic conditions in the streams nor to the predictions of the River Continuum Concept.

Sources of confusion can arise in studies linking invertebrate community organization to food availability or riparian conditions, and reference has already been made to the fact that standing stocks of algae or detritus can give a misleading impression of productivity or rate of food supply and food quality. An additional major source of error in studies of functional feeding groups is incorrect dietary categorization. There is evidence that benthic macroinvertebrates (especially insects) may be opportunistic detritivores feeding on a variety of food materials and particle sizes (DUNCAN & BRUSVEN 1985). This may have the effect that the same invertebrates differentially utilize allochthonous and autochthonous materials in streams experiencing different degrees of shading (ROUNICK *et al.* 1982), with the effect that drastic community shifts will not be evident as the food base changes. In the Hong Kong study streams, species complement changed considerably between sites, with less than 10% of the 30 most numerous taxa occurring in all four streams (DUDGEON 1988a). In these streams it seems likely that opportunistic dietary switches in different habitats would have caused only small errors in estimation of functional group densities, as few taxa were numerous at more than one site. However, some inaccuracies in functional group designation may have occurred if there was significant individual variation in diet among members of a particular taxon.

Land-water interactive systems

Data from Hong Kong and elsewhere indicate that it is inappropriate to consider running waters in isolation from their watershed (LIKENS & BORMANN 1974; LIKENS *et al.* 1977; DUDGEON 1987c), and this notion is a cornerstone of the River Continuum Concept. It is clear that all of the Hong Kong running waters described herein are influenced by the terrestrial landscape, and in unpolluted streams the extent of this influence is a reflection of geology (contributing nutrients) and the type of riparian vegetation (determining the balance between autochthonous and allochthonous energy sources). In polluted sections of Lam Tsuen River, transfers of material from land to water are supplemented by inputs of organic matter in the form of domestic and agricultural wastes. This refuse degrades water quality and eliminates certain taxa while the abundance of a few others is enhanced by the increase in food availability. Land-water interactions in the Lam Tsuen River are dominated by the magnitude of transport of material from the terrestrial environment, with little reciprocal transfer from water to land (DUDGEON 1987c). Thus man's disruption of the natural terrestrial landscape affects the aquatic environment through the excessive transfer of organic compounds and associated nutrients from land to water.

By contrast, the ecology of streams receiving greater or lesser amounts of allochthonous detritus from the terrestrial environment can involve movements of material (especially nutrients) from water to land. Such transfers may occur when the trailing roots of riparian vegetation take up nutrients (FITTKAU *et al.* 1975,

DUDGEON 1984c), and extensive areas of submerged root mats on the bottom and at the sides of streams are a notable feature of some electrolyte-poor waters (FITTKAU *et al.* 1975). The emergence of adult aquatic insects serves as an additional conduit for water to land transfers. This emergence returns energy and nutrients to the land (JACKSON & FISHER 1986; GRIMM 1987), adult insects ultimately entering terrestrial food chains (in the food of spiders, predatory insects, birds and bats) or decomposition cycles (BUSBY & SEALY 1979; DUDGEON 1984c; SWIFT *et al.* 1985; CLARK 1986; ZIMMERMANN & SPENCE 1989; HARRIS 1990). The fact that adult aquatic insects contribute significantly to the total arthropod assemblage in the neighbourhood of the riparian zone (JACKSON & RESH 1989), indicates that they may play important role in the terrestrial food web.

Complementary to the transfer of material from water to land, is the view that the communities of unpolluted streams are structured to utilize their food supply efficiently so minimizing downstream losses to the estuary (VANNOTE *et al.* 1980). Indeed, there are suggestions that the high species diversity that is characteristic of Amazonian rain-forest streams has the function of '... reduction or minimization of nutrient losses ...' and 'communities in the rivers ... act as highly efficient nutrient traps' (FITTKAU 1983). The slowing of downstream export in streams is thought to result from the capture and egestion of organic material by filter-feeders, the production of faeces by these animals and shredders, and the reingestion of these faeces by detritivores further downstream. Shredders in stream headwaters are especially important, because their densities influence litter-processing rates and thus affect the export of fine particulate organic material to consumers downstream (CUFFNEY *et al.* 1990). Ultimately, detritus – and the nutrients it contains – is cycled through the bodies of numerous invertebrates, becoming more completely mineralized with each step in the transfer; its downstream export is thereby retarded. This process of reuse of allochthonous material in streams has been termed spiralling (WALLACE *et al.* 1977) and may contribute significantly to the tightness of nutrient cycles and retentiveness of the lotic community (NEWBOLD *et al.* 1983a, 1983b). The detritus itself can play an important role in this process, because organic debris dams which obstruct water flow tend to promote the retention of particulate matter in the blocked reaches (BILBY 1981; SMOCK *et al.* 1989) and thereby affect macrobenthos abundance and community structure (SMOCK *et al.* 1989). Removal of such dams reduces the ability of the stream to retain leaf-sized particles (BILBY & LIKENS 1980) and increases seston export (BILBY 1981), so that the cleared reach functions like a pipe with allochthonous inputs being flushed downstream. Snags and other woody debris are also a major habitat type and source of food for invertebrates and fishes in low-gradient rivers (BENKE *et al.* 1985; BENKE & WALLACE 1990).

Upstream migrations by fishes, which feed on stream invertebrates and the stored nutrients their bodies contain, can also slow or reverse downstream losses (HALL 1972). Consumption of fish by terrestrial piscivores (birds, etc.) may be a significant mechanism of water to land nutrient transfer. Furthermore, there is now evidence of the general occurrence of directed upstream flights by adult stream insects (MÜLLER 1982). However, data from Tai Po Kau Forest Stream and elsewhere provide supporting evidence of this behaviour in some species, but not others (HARRIS & MCCAFFERTY 1977; NISHIMURA 1981; DUDGEON 1988b; JONES & RESH 1988).

II Populations

Life cycles and population dynamics in a seasonal tropical environment

Life-cycle events and fluctuations in the abundance of north-temperate aquatic animals are often seasonally linked, and periodic phenomena are also known in tropical faunas (STATZNER 1976; WOLDA 1988; SO & DUDGEON 1990), even those in apparently nonseasonal environments (McELRAVY et al. 1982; WOLDA & FLOWERS 1985). Such phenomena may reflect rainfall patterns (TANAKA & TANAKA 1982), but other factors such as light intensity (STATZNER 1976), phases of the moon (HARTLAND-ROWE 1955), or photoperiod (WOLDA 1989) may play a role. It has become clear that one cannot make general statements about the seasonality of tropical animals (WOLDA 1988), whether terrestrial or aquatic. For many tropical animals, the factors determining seasonality (and hence population dynamics) remain a matter for conjecture and speculation (WOLDA 1989).

Temperature plays a major role in the ecology of aquatic organisms (HYNES 1970; WARD & STANFORD 1982), but the influence of temperature will be modified by responses to covarying environmental parameters. The tropical dry season is an adverse period for many terrestrial animals (WOLDA 1988, 1989) but, where water bodies do not dry out, the effects of a dry spell on freshwater organisms is difficult to determine. Summer spates associated with monsoonal rains can scour the stream bed so affecting the entire lotic biota (HYNES 1970; FISHER et al. 1982), and it may be appropriate to view the wet season as a inimical time for running-water species. Indeed, declines in the abundance of benthic macroinvertebrates are frequently associated with spates in Asian rivers and streams (BISHOP 1973; BRIGHT 1982; DUDGEON in press).

The following sections consider the population dynamics of freshwater animals with particular reference to seasonal changes in Hong Kong's climate. An attempt will be made to assess the relative influence of fluctuations in temperature and rainfall. However, increased rainfall and stream flow during the summer are accompanied by rising temperatures and longer days, and interpretation of the independent effects of these parameters on population dynamics are therefore confounded.

The Hong Kong climate

Hong Kong's climate is characterized by cool, dry winters and warm, wet summers. This pattern reflects the influence of the hot humid air of the summer monsoon blowing from the south or southeast, and the winter northeast monsoon which

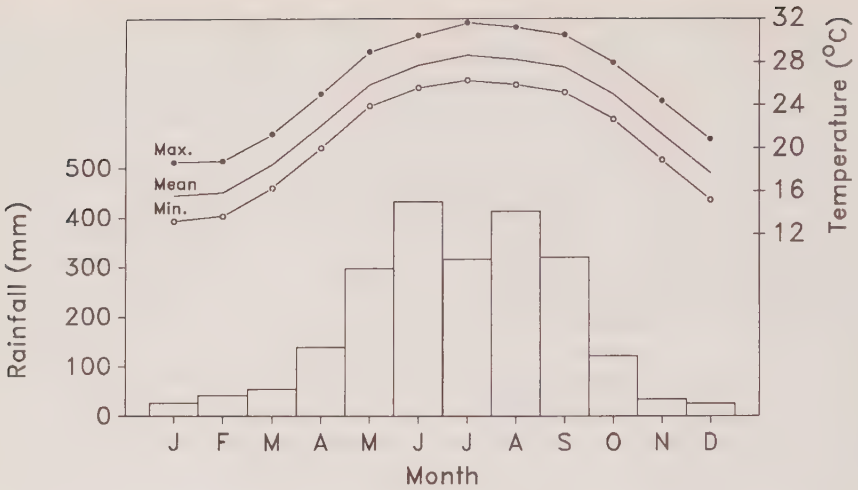


Fig. 16. Mean monthly air temperatures, including mean minimum and mean maximum, in Hong Kong for the years 1951–1980. Monthly total rainfall (mm) over the same period is also shown. Data derived from Royal Observatory (Hong Kong Government) reports (Hong Kong Government 1990).

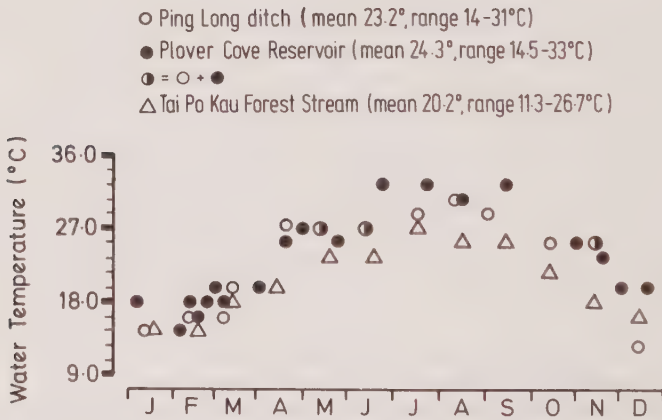


Fig. 17. Seasonal water-temperature changes in Tai Po Kau Forest Stream (1978–79, mean of three sites), Plover Cove Reservoir (1978–79, mean of two sites) and an irrigation ditch at Ping Long, Lam Tsuen Valley (1982–83).

brings cold dry air from Siberia or northern China. Temperatures range from a January mean-minimum of 13.2 °C (Fig. 16) to a July mean-maximum of 31.6 °C (daily mean 1951–80 = 22.8 °C) (Royal Observatory, Hong Kong 1990). Marked seasonal changes in temperature are characteristic of Hong Kong freshwaters (Fig. 17), and are likely to have a major influence on the population dynamics of freshwater animals. However, absolute temperatures as well as diel and seasonal

amplitudes and rates of change may all play a role (WARD & STANFORD 1982). The mean diel range of air temperatures is 5.2°C (annual range $4.8 - 5.6^{\circ}\text{C}$), less for water temperatures ($< 2^{\circ}\text{C}$ in Tai Po Kau Forest Stream, DUDGEON 1988c) although such fluctuations will be greater in unshaded streams compared to those surrounded by riparian vegetation (EDINGTON 1966; WARD 1985). The mean annual degree days (summation of thermal units) for the years 1977 - 1984 was 8394 (Fig. 18). Using 7.8°C (the lowest recorded daily temperature, 1977 - 1984) as equivalent to 'physiological zero' and indicating a possible lower threshold for growth and activity, the annual degree days would be 5547 (DUDGEON 1988c). It is thus obvious that the annual thermal scope for growth of animals in Hong Kong freshwaters is high, but it is also clear that relatively low winter temperatures could influence growth and life-cycle events.

Rainfall, and hence stream discharge volume, will have an important influence on the population dynamics of the lotic fauna. The average annual rainfall is 2224.7 mm, but can exceed 3000 mm in unusually wet years. Approximately 84% of the

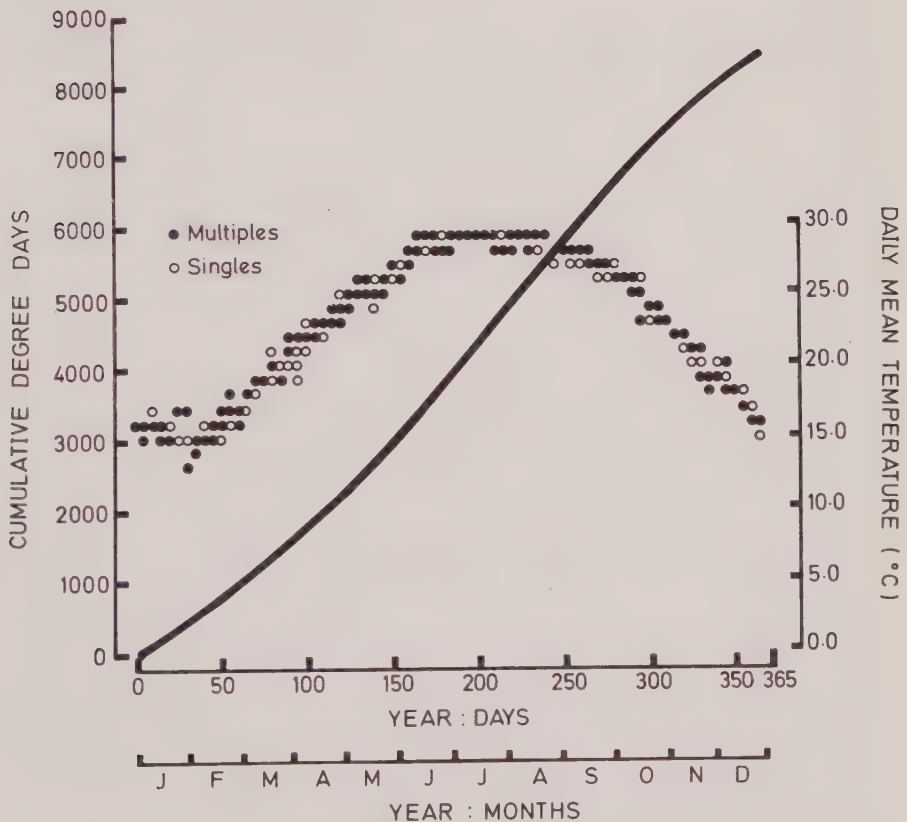


Fig. 18. Average daily mean air temperatures and cumulative degree days in Hong Kong between 1977 and 1984. Calculated from raw data derived from Royal Observatory (Hong Kong Government) reports.

average annual rainfall occurs between April and September (the wet season), about 3% in winter (December to February), and approximately 18% – more than twice the monthly average – in August (Fig. 16); 25% of the rainfall is associated with tropical cyclones. Runoff and stream discharge volume are determined by seasonal patterns of precipitation, and dry-weather flow during the winter months is significantly lower than flood flows resulting from monsoonal rains and typhoons during the wet season (JAYAWARDENA & PEART 1989).

Evidence of seasonal variation in discharge volume is apparent from comparison of the ratio of runoff during the wet season with that in the dry season (October to March). Data are available for seven Hong Kong catchments, and values of this 'seasonality index' range from 2.4 to 29.2 (JAYAWARDENA & PEART 1989; M. PEART, pers. comm.), indicating both a strong seasonal effect as well as evidence of spatial variation in rainfall and runoff. If the maximum daily runoff or stream discharge is expressed as a percentage of total annual runoff, an indication of the intensity of spates can be obtained. In the Shek Pi Tau basin, northern New Territories, which at 27.9 km² constitutes the largest upland catchment in Hong Kong, the maximum daily flow accounts for just under 10% of annual discharge (JAYAWARDENA & PEART 1989). Values for other catchments are less extreme (mean = 4.2%), but nevertheless indicate the highly 'pulsed' nature of flow in Hong Kong streams.

Mollusca

The population dynamics of freshwater molluscs in Hong Kong has been studied in some detail, but there is little evidence of consistent seasonal responses to temperature or stream discharge. Three species of small pisidiid bivalves occur in lowland, slowflowing streams: *Musculium lacustre*, *Pisidium clarkeanum* and *P. annandalei*. The predominately holarctic species, *M. lacustre*, exhibits two periods of recruitment per year, in spring and autumn, which represents life-cycle completion by two overlapping generations. The spring recruits give birth to the fall recruits which in turn give birth to the succeeding spring recruits (MORTON 1985). This ovoviviparous species is essentially temperate-zoned but has a distribution extending southwards into the tropics. Temperatures in Hong Kong do not seem to limit growth or reproduction of *M. lacustre*, and the timing of recruitment may be seen as a strategy to reduce mortality of newly-released larvae. Peaks of recruitment precede and immediately follow the wettest months in Hong Kong, so minimizing the chance of larvae being swept away during spates. The Hong Kong *Pisidium* spp. reproduce throughout much of the year, and three breeding periods (summer, winter and spring) have been identified (MORTON 1986). Each represents reproduction by a separate generation, with most individuals dying after breeding, although some *P. clarkeanum* may survive long enough to produce a second brood. Typically, the summer peak in recruitment is small because of flooding and thus high larval mortality (MORTON 1986). *Pisidium* seasonality appears to result from a short life span rather than climatic constraints on growth and reproduction.

The epifaunal freshwater mussel, *Limnoperna fortunei* (Mytilidae), was introduced into Hong Kong, via piped water, from the Pearl River, southern China (MILLER & MCCLURE 1931; MORTON 1975). It now occurs in Plover Cove Reservoir, in pipelines to and from the reservoir, and has spread to a few streams. Larval settlement occurs twice each year, in summer (June – August) and in winter

(November – December) when water temperatures are approaching maximum and minimum respectively (MORTON 1977a). Like *L. fortunei*, the infaunal clam *Corbicula fluminea* (Corbiculidae) inhabits lentic and lotic waters. It also breeds twice a year, producing larvae in spring and autumn (MORTON 1977b). It is of interest that the expression of sexuality of *C. fluminea* differs between habitats: lotic populations comprise equal numbers of hermaphrodites and females, but the Plover Cove Reservoir population includes males and females in addition to hermaphrodites (MORTON 1983). The relative importance of the hermaphroditic strategy in streams may reflect the frequency of catastrophic mortality caused by spates, and the success of monoecious individuals in recolonizing depopulated areas.

Studies on the population dynamics of bivalves in Hong Kong running waters yield no clear indication of a uniform response to climate, although some evidence of life-cycle strategies which ameliorate the effects of spate-induced mortality can be adduced. Additional data on bivalves from lentic or large lotic habitats (the Pearl River, southern China) do not indicate any general pattern of seasonality: *Corbicula fluminalis*, for example, breeds in winter (MORTON 1983), while *Anodonta woodiana* (Unionidae) females release glochidia larvae in early summer; males have mature gonads throughout the year (DUDGEON & MORTON 1983). Larvae of the latter species are ectoparasites of certain fish (DUDGEON & MORTON 1984), and reproductive timing (May – July) may reflect host availability rather than a climatic constraint on recruitment.

A similar diversity of seasonal population changes are apparent from investigations of gastropods in Hong Kong streams. Among temperate pulmonate snails, oviposition in spring is stimulated by a rise in water temperature above some critical threshold; reproduction ceases when temperature falls below that level in autumn (RUSSELL-HUNTER 1964; McMAHON 1975). Towards lower latitudes, the warm season lengthens and increases the duration of the breeding season. As a result, species producing one generation per year in the northern part of their range, produce two or more in warmer southern climates (McMAHON 1975). Year-round breeding of certain pulmonates is possible in the tropics (BARBOSA & OLIVIER 1958; BLAIR & FINLAYSON 1981), and here temporal changes in snail population size may be associated with the timing of the dry or wet seasons, and the consequent floods and droughts (McCULLOUGH 1957; BARBOSA & OLIVIER 1958; HARRISON & RANKIN 1978; FASHUYI 1981).

The most detailed information on any pulmonate snail in Hong Kong concerns the exotic species *Biomphalaria straminea* (Planorbidae) which originates in Central and South America. This species inhabits irrigation ditches, flooded furrows, slow-flowing streams and the lower course of rivers in Hong Kong (YIP 1983, 1990; DUDGEON 1983a). Changes in the size of populations inhabiting ditches and flooded furrows reflect a near-cessation of breeding activity in winter leading to declines in abundance, and population crashes in the summer which appear to be related to resource depletion at high (approximately 20000/m²) densities (YIP 1983). In streams and rivers, flow volume – and hence rainfall – determines *B. straminea* abundance. These and other pulmonate snails are numerous in stony reaches of the Lam Tsuen River during the dry season; they were confined to weedy areas in the lower course of the river (now modified by human activities), where hydraulic stress was reduced, during the remainder of the year (DUDGEON 1983a). Such data reaffirm the results of studies elsewhere demonstrating that stream

gradient (HARRY & CRUMBIE 1956) and periodic spates or scouring (HARRISON & RANKIN 1978) are important criteria of lotic habitat suitability for pulmonates.

Breeding activity of other pulmonate snails in Hong Kong is reduced during the winter months. Nevertheless, oviposition by common species (*Hippentis cantonensis*: Planorbidae; *Physella acuta*: Physidae; *Radix auricularia plicatula* and *Austropeplea ollula*: Lymnaeidae) occurs, albeit at a reduced rate, at water temperatures of 12 °C (YIPP 1983). High pulmonate densities in the middle and lower course of the Lam Tsuen River during the dry season indicate that cool winter temperatures do not restrict population growth under otherwise favourable circumstances (DUDGEON 1983a).

Most information on Hong Kong prosobranchs is derived from studies of the ovoviviparous family Thiariidae, which includes two parthenogenetic members: *Melanoides tuberculata* and *Thiara scabra*. These two species occupy a variety of habitats in Hong Kong (DUDGEON 1989a), but are generally absent from fast-flowing hillstreams where a third Hong Kong thiarid, *Brotia hainanensis*, abounds. *Thiara scabra* is the rarest of the three, and has only been recorded from Plover Cove Reservoir (DUDGEON 1983c, 1989a) and the lower course of the Lam Tsuen River. Regrettably, water-level fluctuations and river channelization have almost eliminated these two populations. The geographical range of *M. tuberculata* and *T. scabra* encompasses eastern and northern Africa, South-east Asia, China, Taiwan and the islands of the Indo-Pacific (YEN 1939; PACE 1973; BRANDT 1974; BERRY & KADRI 1974; STARMÜHLNER 1979; BROWN 1980), and the former species may even occur in brackish waters (LIVSHITS & FISHelson 1983; LEE 1989). *Brotia hainanensis* is restricted to south-east Asia, and members of the genus occur in the Philippines, Malaysia, Thailand and southern China (DAVIS 1971; BRANDT 1974; DUDGEON 1982b).

The fact that Hong Kong thiarids occupy different habitats has implications for their population dynamics. *Melanoides tuberculata* and *T. scabra* are relatively short-lived (most individuals surviving less than two years), and age-specific mortality is high among the older age classes (DUDGEON 1989a). By contrast, *Brotia hainanensis* has a life-span of approximately 3.5 years, and mortality is age-independent until late in life. Both *M. tuberculata* and *T. scabra* mature early and have one period of recruitment per year, however the pattern of age-specific mortality is such that most individuals did not survive to participate in second breeding season. Both species are ovoviviparous live-bearers with populations consisting entirely of females; in addition, *M. tuberculata* carries mature young in the cephalic brood pouch throughout the year. Release of young by *M. tuberculata* occurs in response to rising temperatures, and juveniles are most abundant during July and August (DUDGEON 1986a). Peak recruitment of *T. scabra* takes place during the coldest months in December and January. Brood size also differs between these two species and is greater in *M. tuberculata* (range = 13–597 eggs or embryos per individual) than in *T. scabra* (5–76) (DUDGEON 1989a).

Overall, *Melanoides tuberculata* is the more widespread and numerous of the Hong Kong thiarids, and has been characterised as an opportunistic or 'fugitive' species (*sensu* HUTCHINSON 1951) which invades new habitats successfully (DUDGEON 1983c, 1986). Early reproduction, large brood size and a lack of males (so that a new population can arise from a single founder female), as well as other characteristics of the species (DUDGEON 1989a), have contributed to the wide geographic range and

eurytopic habitat occupancy of *M. tuberculata*. In addition, reproductive timing can vary according to prevailing temperatures: where these remain high throughout the year reproduction is continuous (e.g. Malaysia, BERRY & KADRI 1974), but hatchling release is periodic in Hong Kong's seasonal tropical climate (DUDGEON 1986).

Brotia hainanensis differs from *M. tuberculata* and *T. scabra* in terms of habitat occupation and population dynamics. It is the only snail that is common in stony hillstreams and the upper course of rivers in Hong Kong. Conditions in such habitats are predictable from year-to-year although unpredictable within years according to the extent and duration of spates brought about by the summer monsoon. As a stenotopic inhabitant of lotic habitats, *B. hainanensis* can be considered an 'equilibrium' species and, as is typical of such animals, it is relatively long-lived (DUDGEON 1989a). Unlike other Hong Kong Thiaridae, *B. hainanensis* is dioecious, with equal proportions of males and females, and grows relatively slowly, attaining maturity at approximately 2.5 years of age. In compensation for separate sexes (i.e. the loss in production of offspring due to the presence of males which contribute sperm but not progeny) and delayed reproduction, females are highly fecund and release > 800 hatchlings at one time (DUDGEON 1989a). Moreover, there are two distinct peaks of hatchling release in each year (DUDGEON 1982d), one preceding and a second immediately following the period of spates associated with the summer monsoon. Repeated breeding and high fecundity may have evolved as a consequence of delayed maturity and the presence of separate sexes in this thiarid, while the timing of recruitment can be seen as an adaptation to reduce juvenile mortality during spates.

The widespread occurrence of thiarids in tropical Asian freshwaters, where they may contribute to a significant proportion of the secondary production (DUDGEON 1986a), could be a result of the habit of brooding eggs and embryos until a crawling, miniature adult snail can be released. The ancestral thiarid was probably a marine snail (LIVSHITS & FISHELSON 1983) and as such had planktonic veliger larvae. Significantly, *Stenomelania* – a fourth genus of Hong Kong thiarid – is confined to freshwater creeks and marshes just above the high tide level and does not penetrate far up streams or rivers. These snails are similar to *M. tuberculata* in appearance and habit, yet they produce planktonic veliger larvae from eggs which hatch in the brood pouch. The turbulence of hillstreams and the downstream loss of larvae would seem to have confined this genus to lowland areas, and such habitat restriction is generally characteristic of Taiwanese *Stenomelania* (PACE 1973).

There is little evidence of a consistent influence of temperature upon the population dynamics of Hong Kong gastropods, and the winter depression in breeding activity seen in pulmonates is not translated into a decline in abundance in habitats such as the Lam Tsuen River. Even within a family – the Thiaridae, for example – there are differences in the timing of recruitment. Some of these differences can be understood in terms of selection pressure: *Brotia hainanensis* lives in hillstreams where recruitment is timed to avoid the main period of spates which could cause juvenile mortality; *Melanoides tuberculata*, which breeds in summer, inhabits slow-flowing streams where spate-induced mortality is less severe. Other differences, such as winter recruitment of *Thiara scabra* versus summer breeding by *M. tuberculata*, cannot be rationalized at present. Ultimately, any explanation of snail population dynamics must include the effects of temperature as well as spates or

scouring, but other factors, such as interspecific interactions, may have a role to play.

Crustacea

The great majority (> 80%) of crustacean species are marine. Among those which have colonized freshwater, members of the order Decapoda (the crabs, shrimps, lobsters and their allies) are the largest and most conspicuous. With the exception of the Palaearctic Astacidae (crayfish or crawfish), freshwater decapods are a tropical phenomenon. In Northern European and American streams, the larger crustaceans are represented by the Isopoda (Asellidae) and Amphipoda (Gammaridae). Hong Kong freshwaters, by contrast, are host to freshwater shrimps of the families Atyidae (*Caridina* and *Neocaridina*) and Palaemonidae (*Macrobrachium*), as well as grapsid, potamid and parathelphusid crabs.

True freshwater crabs are those which spend their entire lives in streams and rivers, and never return to the ancestral marine habitat. A variety of estuarine or mangrove crabs may move into entirely fresh waters (e.g. *Varuna litterata*: Grapsidae), but they are occasional visitors and cannot reproduce in such habitats. Most grapsids are denizens of mangroves or the intertidal zone. Nevertheless, members of the genus *Eriocheir* (the hairy-clawed or mitten crabs) spend most of their lives in freshwater, returning to the sea to release their eggs which hatch into planktonic zoea larvae. It is during the autumn mating season, when their gonads are ripe, that the Chinese mitten crabs (*Eriocheir sinensis*) are collected for food. Although they are most delicious when lightly cooked, mitten crabs serve as intermediate hosts of the lung fluke (*Paragonimus*) and gourmets risk parasitic infection if they consume half-raw crabs. *Eriocheir japonicus*, is smaller than *E. sinensis* and is widespread in Hong Kong although not generally collected for human consumption.

The true freshwater potamid (not Potamonidae, see NG 1988) and parathelphusid crabs, by contrast to grapsids, spend their entire lives in freshwater. *Somanniathelphusa sinensis* (Parathelphusidae), the commonest Hong Kong species, is widespread in China and Taiwan (DAI & CHEN 1979; HWANG & MIZUE 1985). This and other freshwater crabs have large (over one millimetre in diameter) yolky eggs, and the planktonic larval stages typical of marine species are suppressed so that hatchlings resemble a miniature adult. The eggs are held in place under the abdomen by the setaceous pleopods, where they are brooded for several weeks. Brooding females are reclusive and retreat into burrows or cavities beneath large stones. Juveniles are released near the onset of the wet season in Hong Kong, and production of young during the monsoon seems to be typical of freshwater crabs in tropical Asia (FERNANDO 1960; PILLAI & SUBRAMONIAM 1984; NG 1988). Regrettably, detailed information on the population dynamics of these animals is lacking.

There is evidence of habitat segregation between potamid and parathelphusid crabs. Potamids, such as *Cryptopotamon anacoluthon* and *Nanhaipotamon hongkongense*, are most numerous in upland streams with clear, fast-flowing water and accumulations of leaf litter, while parathelphusids inhabit riverine habitats and slow-flowing low-gradient streams where they dig burrows in mud and clay banks. Despite different habitat occupancy, both crab families exhibit similar life cycles with suppressed planktonic development and hatchlings that resemble tiny adults.

Among freshwater shrimps, the relatively large *Macrobrachium* species (Palaemonidae) occur in completely fresh water as well as in high-salinity brackish water (JOHNSON 1961a). The Hong Kong species differ in their tolerance of (or requirement for) salt, and dwell in a range of habitats. This diversity has a significant influence on shrimp life histories. *Macrobrachium hainanense* is distributed widely from southern China to Java (YU 1931; HOLTHUIS 1952) and inhabits hillstreams far from the sea (DUDGEON 1985a). The species spends its entire life in fresh water, adults taking up guarded territories in midstream areas while juveniles occur among trailing vegetation along the stream banks. *Macrobrachium nipponense* is likewise widely distributed, extending northward to Japan. These shrimps tolerate brackish water and occur in tidal shrimp ponds (as in the Mai Po Marshes of Hong Kong) as well as in larger rivers and reservoirs. *Macrobrachium nipponense* can complete its life cycle in brackish or entirely fresh water (WONG 1987). *Macrobrachium formosense* has also been recorded in Hong Kong reservoirs.

Although ovigerous females of many *Macrobrachium* species undertake a seaward migration for mating, this is not always a necessity. Indeed, *Macrobrachium nipponense* shows an increase in egg size and larval survival, a shortening of larval stages, and a decrease in clutch size and larval duration for freshwater compared to brackish-water populations in Japan (MASHIKO 1983a; WONG 1989). In addition, the growth rate of females in freshwater populations is noticeably depressed, although one-year-old ovigerous individuals can be found in both brackish and freshwater habitats during the warmer months (MASHIKO 1983b; OGAWA & KAKUDA 1986). Male *M. nipponense*, by contrast, do not attain sexual maturity until two years of age, and the delay in reproductive activity may be associated with the development of cheliped sexual dimorphism. *Macrobrachium* males bear larger second chelipeds than the females, and the female is guarded between the long chelipeds of the male during pair formation. Interference with the pairing individuals is reduced by the male nipping the intruder with his large chelipeds (MASHIKO 1981). In addition, because the female moults immediately before spawning, the large chelipeds of the male have an important role in fending off cannibalistic attacks on his soft-shelled mate (MASHIKO 1981).

Like *Macrobrachium nipponense*, stream-dwelling *M. hainanense* in Hong Kong begins breeding in late spring and ovigerous females are found in May and June (DUDGEON 1985). Reproduction seems to be stimulated by rising water temperatures, and the abundance of *M. hainanense* in the Lam Tsuen River is positively correlated with water temperatures prevailing one and two months earlier. Unlike *M. nipponense*, *M. hainanense* has an abbreviated larval development (WONG 1989) lacking the planktonic stages seen in the former species. The suppression of larval stages may be a selective advantage for species which produce young close to the onset of the wet season when streams are subject to spates.

Atyid shrimps occur in freshwaters and low-salinity brackish waters (JOHNSON 1961a, 1961b). Two rather diminutive (<3 cm body length) species are found in Hong Kong streams: *Caridina lanceifrons* and *Neocaridina serrata*. Both inhabit streams and small rivers (where they congregate among trailing vegetation), but are sensitive to pollution and confined to clean sites. The two species may occur in the same habitat, but *N. serrata* is more widespread and abundant. Unlike some other atyids (e.g. certain *Caridina* spp.: BENZIE 1982), both shrimps breed in fresh water (MIZUE & IWAMOTO 1961; SHOKITA 1976; DUDGEON 1987d) and have abbreviated

larval development, producing hatchlings in an advanced stage of growth (MIZUE & IWAMOTO 1961; DUDGEON 1987d). This may be an adaptation to reduce washout of larvae during wet-season spates, and it is significant that ovigerous females of *N. serrata* occur from April to October (DUDGEON 1985), a period including the summer monsoon. An alternative or supplementary explanation is that freshwater decapods produce larger eggs (from which well-developed juveniles hatch) than their marine relatives in response to the paucity of planktonic larval food in streams (WONG 1989).

Neocaridina serrata are rather short-lived with a maximum longevity of approximately 12 months. Consequently, each individual participates in only one summer breeding season, although females may spawn more than one batch of eggs during that time. As recorded for *Macrobrachium hainanense*, the abundance of *N. serrata* in the Lam Tsuen River was significantly correlated with water temperature (DUDGEON 1985). A similar relationship has been noted for *Caridina singhalensis* in Sri Lankan Mountain streams (DE SILVA 1982). Warmth stimulates reproduction in *N. serrata*, and ovigerous females were only recorded when water temperatures exceeded 20 °C. In addition, there was a correlation between the percentage incidence of brooding females and prevailing temperatures (DUDGEON 1985). A hypothesis involving stimulation of breeding by rising temperatures gains support from the observation that Japanese *Caridina* and southern United States *Macrobrachium* reproduce in summer (KAMITA 1956, 1957, 1959; TRUESDALE & MERMILLIOD 1979). In tropical regions with equable temperatures, recruitment of freshwater shrimps occurs throughout the year (BABU 1963; HART 1981), although 'hot season' peaks in the abundance of ovigerous females have been recorded (HART 1980). This pattern may be altered in regions with a marked wet season where reproduction is synchronized with the onset of the rains (RAMAN 1967; ABELE & BLUM 1977; RAJYALAKSHMI 1980).

Summarizing, it appears that freshwater decapod reproduction in seasonal tropical or subtropical regions is confined to those months when streams are warm enough ($> 18 - 20^{\circ}\text{C}$) to permit gametogenesis or embryonic development, the latter being temperature dependent (HART 1981). In the equatorial zone, breeding can proceed throughout the year but secondary restraints may be imposed where, for instance, habitat availability for juveniles is periodically limiting (RAJYALAKSHMI 1980); in such situations reproduction is synchronous with the wet season. Temperature seems to be the main factor determining the reproductive seasonality and population dynamics of freshwater shrimps in Hong Kong, and this has the repercussion of synchronizing breeding with the summer monsoon. As a result, abbreviated development which reduces the downstream loss of larvae during spates attains special importance.

Insecta

Little is known of the seasonality or population dynamics of tropical stream insects; this is especially true in Asia. While the emergence patterns of some Japanese taxa (Trichoptera, for example) have been relatively well documented (e.g. NISHIMURA 1966, 1976; GOSE 1970; ITO 1987; TANIDA 1980), data from more southern latitudes are scarce. Adults of some taxa showed seasonal flight patterns in a Malaysian

stream (BISHOP 1973), while others were present as pupae throughout the year. However, there is evidence that flight periods of caddisflies and mayflies may be discontinuous – even in ‘aseasonal’ tropical areas (STATZNER 1976; McELRABY et al. 1982; WOLDA & FLOWERS 1985). Flight of aquatic insects with long-lived adults (such as some beetles and heteropteran bugs) is often associated with monsoonal rains and – in Sri Lanka, for example – is a strictly seasonal phenomenon restricted to relatively few days in the year (FERNANDO 1958, 1959, 1961). In general, monsoonal rains are accompanied by winds of considerable speed providing an ideal situation for the dispersal of aquatic insects. The climatic conditions during the monsoonal rains are accompanied by winds of substantial speed providing a considerable distances by wind currents (FERNANDO 1961).

The behaviour of adult aquatic insects is relevant to seasonality, particularly with regard to whether swarming and synchronized mass emergence is observed in species – such as mayflies – which have short-lived adults. Swarming behaviour is more common in temperate than tropical regions. Predation by dragonflies and birds is intensive in the lowland tropics (BISHOP 1973; EDMUNDS & EDMUNDS 1979), and many species of mayflies emerge as subimagos in the first two hours of darkness, transform into imagoes before dawn, and mate and oviposit by mid-morning. Seasonal coordinated mass emergence has evolved in a few tropical mayflies (EDMUNDS & EDMUNDS 1979), as well as some temperate ones, possibly as a mechanism for satiating predators (SWEENEY & VANNOTE 1982). All tropical mass-emergent species swarm over rivers (EDMUNDS & EDMUNDS 1979), while others lacking such synchronization exhibit nuptial flights some distance from the larval habitat. Such behaviour may function as a means of avoiding concentrations of predators near streams, rivers or lake margins.

Most data on the seasonality and population dynamics of lotic insects in Hong Kong concern Odonata, and four species have been investigated: the damselfly *Euphaea decorata* (Euphaeidae), and the dragonflies *Zygonyx iris* (Libellulidae), *Heliogomphus scorpio* and *Onychogomphus sinicus* (Gomphidae). All species are univoltine, completing one generation per year. Adult flight periods of *E. decorata* begin in late April or early May and adults are abundant until September, with a few individuals persisting until October (DUDGEON 1989b). Larval recruitment begins in June and growth continues throughout the year. This pattern appears to be rather consistent from year-to-year (DUDGEON 1989b). Data on other damselflies, although less detailed, indicate a similar pattern: *Rhinocypha perforata* (Chlorocyphidae [= Libellaginidae]) adults occur from May to September, but a few individuals may be recorded in April, October and November; adult *Mnias mneme* and *Neurobasis chinensis* (Calopterygidae) emerge in April, although the flight period of the former species is no more than a month.

Like *Euphaea decorata*, *Zygonyx iris* is univoltine with adult emergence from April to June (DUDGEON & WAT 1986). The flight period appears to last at least until August (ASHINA 1965). Emergence of both species of gomphid dragonflies peaks in May, although the presence of larval exuviae of *Onychogomphus sinicus* on rocks around Tai Po Kau Forest Stream indicate that some adults fly during late April (DUDGEON 1989e). Gomphid adults do not remain close to emergence sites (KUMAR & PRASAD 1981), and thus the duration of the flight period is difficult to determine with certainty. Gomphidae from Indian hillstreams spend three to four months as adults (KUMAR 1976), and available data on Hong Kong species are in accordance

with this. Although there is good evidence that *O. sinicus* and *H. scorio* are univoltine, first-stage gomphid larvae are present in Tai Po Kau Forest Stream throughout the year (DUDGEON 1989e). This could be indicative of undetected adult emergence and subsequent oviposition, but staggered hatching of eggs laid in summer would give rise to a similar pattern.

The life cycles of Hong Kong Odonata seem to be typical of dragonflies and damselflies inhabiting perennial streams in the tropics. Adult emergence begins before the onset of the summer monsoon which may reduce damage or wash-out of large larvae during summer spates. Timing of emergence could, however, reflect an influence of rising water temperatures on larval maturation. Nevertheless, many dragonflies in Indian hillstreams are univoltine and adult emergence in summer is timed to precede the monsoon, thereby reducing spate-induced mortality of larvae (KUMAR 1976). Available information does, in fact, indicate that odonate reproduction in the tropics coincides with seasonal rains (CORBET 1980, 1981).

While the seasonality of some Hong Kong Odonata is relatively straightforward, this is not true of at least one species – the migratory *Pantala flavescens* (Libellulidae). These insects migrate across the Old World tropics, and huge swarms arrive in Hong Kong during early summer. Some of these individuals mate and oviposit in temporary pools and ponds but the swarms soon move on. The dragonflies return in early autumn, at the end of the wet season, when swarms are joined by emerging larvae that have developed during the summer months. Some weeks later the insects move on and are not seen again until the following year. The phenomenon of migration by *P. flavescens* has been well documented (CORBET 1980), but the distance flown by individuals, their flight routes, and the length of adult life are not known.

The seasonality and population dynamics of Hong Kong caddisflies (Trichoptera) presents quite a different picture from the relative uniformity exhibited by Odonata. Disparity in life-cycles is shown well by a comparison of Stenopsychidae and Macronematinae (Hydropsychidae) which, by virtue of their size and (in the latter case) bright colours, are conspicuous components of the caddisfly fauna. Both groups are widely distributed in Asia, the Stenopsychidae – which attains its greatest diversity in Palaearctic Asia – decreasing in species richness towards the equator (DUDGEON 1987a). By contrast, Macronematinae are well represented in the Oriental tropics (ULMER 1951; BARNARD 1980). Among the Macronematinae, *Polymorphanisus astictus* has the longest flight period lasting from late April until mid-September (DUDGEON 1988b). *Macrostemum fastosum* begins flying at the same time as *P. astictus*, but becomes scarce in July. *Macrostemum lautum* adults are present only in mid-May, and this pattern is consistent among years (DUDGEON 1988b). Adult *Stenopsyche angustata* occur throughout the year and show no evidence of seasonality.

Available data suggest that macronematine caddisflies are univoltine in Hong Kong, but there are few clues as to the voltinism of *S. angustata*. Some *Stenopsyche* species are bivoltine in Japan (NISHIMURA 1966), but certain species produce either one or two generations a year according to temperature regime (GOSE 1970). In view of high value of annual thermal scope for growth (DUDGEON 1988c), *S. angustata* may be polyvoltine in Hong Kong (completing several generations per year) but studies of larval development are needed to elucidate this point.

Macronematine adults are most numerous in Tai Po Kau Forest when daily air temperatures exceed 25 °C, and water temperatures (measured at dusk) are above

20 °C increasing toward the annual peak of 26 °C attained in August (DUDGEON 1988b). It is tempting to suggest that early summer emergence of Macronematinae represents a response to rising water temperatures, but there is no direct evidence for this. In view of the fact that stenopsychids are primarily a Palaearctic group while the Macronematinae (especially the genus *Polymorphanisus*) are more typical of warm running waters, it is possible that developmental responses to temperature may confine macronematine emergence to the summer months in Hong Kong's seasonal tropical climate, while the cool-adapted (*sensu* Ross 1956) Stenopsychidae could fly throughout the year. Early summer emergence of Macronematinae could also result from selective pressures to reduce spate-induced mortality of final-instar larvae and pupae during the wet season. Even if reduction of pre-emergence mortality ultimately determines the timing of emergence, rising water temperatures could nevertheless serve as a proximal cue.

A third pattern of seasonality is exhibited by the polyvoltine caddisfly *Anisocentropus maculatus* (Calamoceratidae). Adults can be collected throughout the year but are scarce in summer. In late autumn and winter, when stream flows are stable or declining, adults are numerous and larvae are concentrated among packs of allochthonous litter in stream pools or in areas of slow-flowing water close to the banks. The larvae construct a flat case comprising two pieces of leaf which they cut from allochthonous litter using their mandibles. The case is cryptic but exposes a large surface area to the current, rendering it vulnerable to being swept away during spates. The seasonal dynamics of this species therefore reflect stream discharge volume rather closely, and populations that build up during periods of low water are subject to catastrophic downstream drift when flows increase. The persistence of a few larvae in sheltered microhabitats during the wet season provides a nucleus for ensuing population increase.

Data on the seasonality of other caddisflies are scarce, but at least some taxa have extended flight periods. Adult Hydroptilidae, for example, can be collected for nine months of the year but are absent during the coldest months. Although there are no clear data on the voltinism of hydroptilids at present, four or more of the ten Hong Kong species may be bivoltine or polyvoltine (WELLS & DUDGEON 1990).

Mayfly population dynamics in Hong Kong have not been investigated intensively. The seasonal patterns which have been observed include Heptageniidae species whose adults fly throughout the year, other mayflies which emerge during the summer (*Ephemera* [*Ephemera*] *spilosa*: Ephemeridae; *Isonychia kiangsinensis*: Oligoneuriidae), and at least one species which shows markedly synchronized emergence in April (*Ephemera* [*Aethephemera*] *pictipennis*). A lack of clear seasonality or synchrony of larval growth is characteristic of some Heptageniidae, Leptophlebiidae and Baetidae, and these mayflies may be polyvoltine. Periods of extended recruitment, multiple overlapping cohorts, and a long period of adult emergence seem to be typical of many mayflies in tropical and subtropical streams (BISHOP 1973; CLIFFORD 1982; FISHER & GRAY 1983; BENKE & JACOBI 1986; CAMPBELL 1986; BUNN 1988; BRITTAIN 1990), and may be usual in streams where water temperatures remain above 15 °C for a major portion of the year (BENKE & JACOBI 1986). Indeed, generation times of approximately one month (less in some cases) have been recorded for mayflies and chironomid (Diptera) larvae growing at temperatures >20 °C (SWEENEY & VANNOTE 1984; BENKE & JACOBI 1986; MAHESHWARI 1989; STITES & BENKE 1989), and there is evidence that baetid

mayflies in tropical streams can complete larval development in less than 30 days (J.D. HYNES 1975a; MARCHANT 1982).

Clearly, high prevailing water temperatures provide the potential for polyvoltinism among Hong Kong mayflies, and it is therefore interesting that not all mayflies exhibit such cycles. One explanation for the seasonal emergence of ephemerids (*Ephemera* spp.) might relate to microhabitat availability. These mayflies burrow into sandy sediments, which are in short supply during the wet season because floods scour the stream bed. Given this scenario, an appropriate evolutionary response might involve emergence from the stream prior to the rains (as in *Ephemera pictipennis*) or during the early part of the wet season (as in *E. spilosa*), ensuring that only eggs or tiny larvae are present when suitable habitat may be limiting.

It is not possible to generalize about climatic influences on the seasonality of stream insects in Hong Kong. Some taxa are polyvoltine, others are univoltine. Both synchronized emergence and aseasonal flight periods have been recorded, and major periods of recruitment may occur in the summer or during the winter. A strategy of emergence in late spring or early summer is common to the Odonata, Trichoptera and Ephemeroptera, and it is noticeable that such seasonality involves relatively large species. Indeed, there is evidence that small larvae are less liable than larger conspecifics to be crushed and mutilated by rolling stones during spates (HARKER 1953). Concordance of life cycles among large species from three insect orders lends support to the suggestion that emergence may be timed to avoid spate-induced mortality of mature larvae, a degree of synchrony arising from physiological responses to temperature and/or increasing day length. Another non-exclusive possibility is that many polyvoltine species possess flexible, poorly-synchronized life histories of the type that are thought to represent an adaptive response to streams with variable and unpredictable discharges (WINTERBOURN et al. 1981; LAKE 1982). However, while the summer monsoon may play an important role in determining the seasonality and population dynamics of certain aquatic insects, and there is evidence suggesting that insect reproductive activities may be adjusted to seasonal flood regimes in some North American streams (GRAY 1981), other factors must be called upon to account for the full range of life cycles observed.

One determinant of seasonality which deserves closer consideration is photoperiod, because it is noticeable that species with highly synchronized emergence (such as *Macrostemum lautum* and *Ephemera pictipennis*) fly on almost the same calendar days each year. Actual values of temperature and rainfall in any one year can vary from those typical of a given month, but day length does not. Accordingly, this factor can serve as a proximal cue for synchronized emergence on the same date each year. Such synchronization may be important for enhancement of mating success in low-density populations, or could serve as a mechanism ensuring that emergence precedes an unusually early arrival of the summer monsoon.

Fishes

There are no detailed data concerning the population dynamics of fishes, amphibians or reptiles in Hong Kong streams, and only preliminary information on the timing of reproduction are available. As would be expected, the activity of these

ectothermic animals is enhanced by elevated temperatures, and breeding of many species is initiated in spring. For example, the presence of large numbers of small (< 2 cm long) loaches (Homalopteridae and Cobitidae) and gobies (Gobiidae) in hillstreams during July and August indicates that reproduction must have been initiated on or before the onset of the summer monsoon. Likewise, breeding by exotic Poeciliidae, which inhabit the lower course of most Hong Kong rivers, is stimulated by rising temperatures. Warmth also increases the frequency of brood production by these viviparous fishes. The length of the breeding season (which involves multiple brood production by females) varies across the geographic range of poeciliids, but given favourable water temperatures they can reproduce throughout the year. Reproduction is initiated by water temperatures above 15 °C, although photoperiod may also influence breeding (MILTON & ARTHINGTON 1983).

In large tropical rivers many species spawn during the early rains, and this is often associated with a migratory phase bringing the fish to flooded areas with a rich food supply which can be exploited by the hatchlings (WELCOMME 1979; PAYNE 1986; LOWE-McCONNELL 1987). Where temperatures do not limit spawning, seasonality is imposed by environmental factors leading to injections of nutrients (as, for example, through flooding and the transfer of material from water to land), or through direct influences such as the effects on fish larvae of turbulence generated by seasonal spates (LOWE-McCONNELL 1987). The staggering of peak spawning times among closely-related sympatric species (SCHUT et al. 1984), or among those sharing the same resources (food or living space), indicate that biotic pressures (such as competition) may determine the seasonality of some tropical fish communities (LOWE-McCONNELL 1987). Elsewhere, temperature appears to be extremely important in regulating reproductive cycles of cypriniform fishes (DE VLAMING 1972), and available data indicate a general correlation between elevated or rising temperatures and breeding activity in Hong Kong stream fishes.

There are data to indicate that certain stream-dwelling North American cyprinid fishes have life histories linked to the periodicity of floods, which can be used as reproductive cues (JOHN 1963). Moreover, given that certain subtropical fishes time breeding activity to precede seasonal spates, so trimming or streamlining the body form and adjusting energy allocation to the increased stream flow (THIBAUT & SCHULTZ 1978), an evolutionary response in reproductive seasonality to ameliorate the effects of spates cannot be ruled out among hillstream fishes in Hong Kong. An extra benefit would derive from not wasting energy in the production of eggs or hatchlings that might be swept away by flood waters.

The effects of spates on stream fishes can depend upon small differences in the timing of reproduction and of flooding (HARVEY 1987). The latter point applies particularly to the paradise fish (*Macropodus opercularis*: Belontiidae); males build a floating bubble nest in which the fertilized eggs are incubated. This species can be collected from trailing vegetation along stream margins where breeding must be scheduled to minimize the chances of nest destruction by spates. Populations of the Hong Kong minnow *Zacco platypus* may also be reduced by flooding, and data from Japan (MIZUNO & NAGOSHI 1964) indicate that reservoir construction along mountain streams increases fish abundance by preventing juveniles from being washed downstream. Significantly, Japanese *Z. platypus* breed in summer, a pattern which – if followed in Hong Kong – would lead to significant spate-induced mortality of hatchlings.

Reproductive timing can alleviate the effects of flooding on fish populations, but mode of development may play a role. One Hong Kong goby, *Tukugobius wui*, represents a genus of fishes that inhabits rapidly-flowing stream and river headwaters (MIZUNO 1960). When compared with genera such as *Rhinogobius* or *Ctenogobius* which occur further downstream, summer-spawning *Tukugobius* produce a small number of large eggs within which the larval swimming stages are passed. The newly-hatched larvae are thus benthic fish with the same body form as the adult (MIZUNO 1960, 1963). This life-cycle has been derived from the type shown by *Rhinogobius* spp. which produce a great number of small eggs that hatch into free-swimming larval stages; development takes place in lakes or (in the case of amphidromous forms) estuaries, although the adult habitat is lowland streams and rivers (MIZUNO 1960). In this context it is significant that the benthic loach *Noemacheilus fasciolatus* also produces a small number of unusually large (approximately 2 mm-diameter) eggs.

Herpetofauna

Hong Kong has a rich amphibian fauna in relation to its land area and, although detailed investigations of life-history and population dynamics have yet to be undertaken, some data on breeding seasonality have been recorded (KARSEN et al. 1986). Only species associated with flowing water will be considered here. Newts (*Paramesotriton hongkongensis*: Salamandridae) occur in hillstream pools and are reported to breed in the cooler weather from November to February. About 120 eggs, which are attached to submerged objects, are laid; hatching takes three weeks or more, and the larvae bear external gills which persist for approximately seven months until metamorphosis into the air-breathing adult form. Larvae are present throughout the winter and spring suggesting that metamorphosis may occur in May.

Many of the 22 species of Anura found in Hong Kong breed during early or late spring, but several species reproduce throughout the year. Tadpoles of the local toads can be seen in all months, but the habits of the two species most closely associated with streams (*Megophrys brachykolos* and *Leptobrachium pelodytoides*: Pelobatidae) are obscure. *Megophrys* tadpoles are reported to ingest particulate material from the water surface, while *Leptobrachium* feed by 'snipping' pieces of allochthonous leaves (INGER et al. 1986).

The most common hillstream frog is *Rana paraspinosa* (Ranidae), which lays single eggs (i.e. not in strands) in pools. Year-round breeding is inferred by the presence of tadpoles during all months, but this observation could also reflect slow larval growth during the cooler months. The reproductive habits of other stream frogs such as *Rana spinosa* (the giant spiny frog), *Rana latouchii* and *Rana livida* are not known, but the cascade frog (*Amolops hongkongensis*) - which is recorded only from the territory - attaches small clutches of pea-sized eggs to wet rock surfaces or submerged boulders. The tadpoles are approximately 2 cm long upon hatching, and can be found in all months of the year. The mouth and lips are modified for attachment to rocks in strong current, and the gut contents comprise periphyton scraped from this substrate. In this species algae are rasped from stone surfaces by rows of horny lip denticles, and the suspended food is concentrated on the gills

before ingestion. Aspects of the ecology of a Malaysian *Amolops* species are described by BERRY (1966) and BULLOCK (1969).

Overall, it is probable that the population dynamics of those frogs which may breed all year round is primarily affected by changes in current and water level, as has been proposed for tropical frogs in aseasonal tropical environments (INGER 1969, INGER et al. 1986). For the remaining species, population size will reflect the interaction of rising temperatures (which stimulate breeding) and mortality of tadpoles during spates. This conclusion accords with studies of frogs in Thailand (some species of which occur in Hong Kong) where rainfall appeared to regulate reproductive patterns in areas characterized by a pronounced dry season (HEYER 1973). The more northerly the environment, the greater the number of factors which controlled breeding in Thai frogs.

Among the reptiles associated with Hong Kong streams are the terrapins *Chinemys reevesi* and *Cuora trifasciata* (Emydidae). The breeding habits of the former species, which is relatively common, are reported to involve pairing in spring followed by females laying four to six eggs in June (KARSEN et al. 1986). The waterside skink (*Tropidophorus sinicus*: Scincidae) is common in and around upland streams. This lizard produces three to six live young in early spring. The water snakes include species of the genera *Natrix* and *Opisthotropis* (Colubridae: Natricinae), which seem to be confined to rocky hillstreams; *Opisthotropis lateralis* is reported to lay eggs in June. *Enhydryis chinensis* (Colubridae: Homalopsinae) is a lowland species which produces live young (up to 13 in a brood) during the summer.

Recapitulation: seasonality of lotic populations

It is futile to expect a simple, synchronized response of the population dynamics of different groups of lotic animals to Hong Kong's seasonal tropical climate. Available information indicates that some species reproduce all year round (e.g. the caddisfly *Stenopsyche angustata*) and, while many species show recruitment during the spring or summer, others (such as the snail *Thiara scabra* and the Hong Kong newt) breed in winter. Emergence timed to precede the summer monsoon is a common pattern for lotic insects, and might be an evolutionary response to minimize spate-induced mortality of large larvae, but this is by no means the only flight pattern recorded around Hong Kong streams.

Reproductive timing and population dynamics will reflect an amalgam of different influences, including those that arise from a species geographical distribution (whether it is primarily a north-temperate or tropical form), evolutionary history, macrohabitat (swift hill streams versus slow-flowing lowland streams), microhabitat (for example, packs of allochthonous leaves – in the case of the caddisfly *Anisocentropus maculatus* – versus stony sediments), and vulnerability to spate-induced mortality. Thus, while rising spring temperatures may stimulate reproduction in certain species, it is naive to suppose that this factor alone will be sufficient to account for the observed diversity in the seasonality of Hong Kong's stream fauna.

Drift of the stream fauna

The incessant downhill flow of water which characterizes streams influences all aspects of the lives of lotic animals. Of these ramifications, one of the most striking is the phenomenon of drift, whereby benthic animals enter the water column and are carried some distance downstream by the current until they settle out. Both entry to, and exit from, the water column can be a passive or active process. Passive initiation of drift is especially common during spates, and involves accidental dislodgement of animals which are swept away by the current; subsequent return to the stream bed may involve active swimming movements, entanglement in snags and other obstacles, or passive deposition in areas of slow flow or dead water. An active return to the substratum is indicated by the observation that dead mayflies drift further during daylight than live ones (CIBROWSKI 1983), although at night live mayflies behave so as to prolong drift (CAMPBELL 1985).

Active entry into the water column – induced by the animal itself – may involve swimming, movements from sheltered sites to those exposed to the full force of the current, or merely releasing hold of the stream bed. Movement that involves direct entry into the water column, or activity which increases the chance of an animal being swept away by the current, gives rise to the phenomenon of behavioural drift. This, it should be noted, is an extensive and heterogeneous category, and may be further subdivided to yield an active drift grouping referring only to behaviour involving direct entry into the water column (BRITTAIN & EIKELAND 1988). Passive or accidental entry into the water column comprises background drift; where this occurs during spates it may be termed catastrophic drift and can lead to significant reductions in benthic population densities (ANDERSON & LEHMKUHL 1968).

Behavioural drift has important implications for the population dynamics of benthic animals (WATERS 1972; MÜLLER 1974). In particular, drift may play a part in the location of suitable food and microhabitat, and facilitate escape from benthic predators, by enhancing dispersal ability. Despite this, not all stream taxa drift. Investigations in Tai Po Kau Forest Stream have shown that elmids and psephenid beetle larvae are under-represented in drift samples relative to their abundance among the bottom sediments (DUDGEON 1983d). Caddisfly larvae (such as the odontocerid *Psilotreta kwantungensis*) with heavy stone cases are likewise under-represented, but glossosomatids (*Agapetus* sp.) – which, rather than extending the old case, must leave their stone case and build a new one upon each moult – are more prone to drift.

Diel periodicity

One feature of behavioural drift is the tendency for most taxa involved to exhibit some kind of diel variation in their drifting activity (TANAKA 1960; WATERS 1972). Species may be either day-time or nocturnal (including crepuscular) drifters, and night-time drift seems to be induced by reductions in light intensity (BISHOP 1969; WATERS 1972). In Hong Kong, night-time elevations in the number of taxa as well as the number of individuals drifting are apparent (Fig. 19), and there is a marked increase in drifting animals soon after sunset. Drift periodicity is strongly nocturnal in most streams (e.g. WATERS 1972; BISHOP 1973; J.D. HYNES 1975b; ITO 1984;

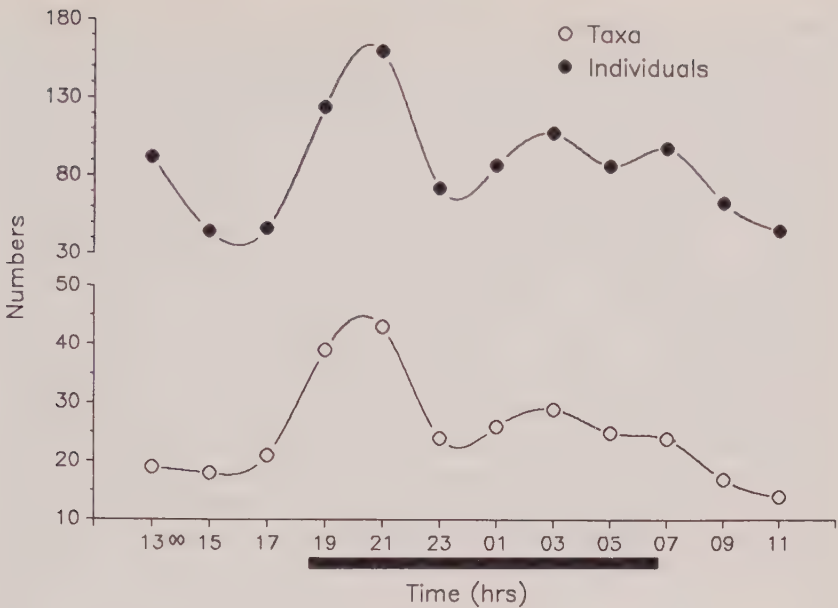


Fig. 19. Diel changes in the number of individuals and taxa drifting in Tai Po Kau Forest Stream (November 1978).

Table 8. Diel drift activity in Tai Po Kau Forest Stream.

Continuously active	— Hydrachnellae, <i>Baetis</i> T ₃ , cf. <i>Neoperla</i> spp., <i>Eoophyla</i> sp., Tanypodinae
Day active only	— none
Day active with dusk or dawn peak	— none
Night active only	— <i>Baetis</i> nr. <i>pseudofrequentus</i> , <i>Ephemerellina</i> T ₁ , cf. <i>Leuctra</i> sp., <i>Agapetus</i> T ₁ , <i>Stenopsyche angustata</i> , <i>Chimarra</i> T ₂ , <i>Cheumatopsyche ventricosa</i> , <i>Cheumatopsyche</i> TdB, <i>Cheumatopsyche</i> cf. <i>spinosa</i> , <i>Herbertorossia quadrata</i> , <i>Hydropsyche chekiangana</i> , <i>Hydropsyche</i> sp., <i>Melanotrichia serica</i> , <i>Pseudoneureclipsis</i> sp., <i>Anisocentropus maculatus</i> , Trichoptera imagines, <i>Helodes</i> #1, <i>Simulium</i> T ₁
Night active with a dusk peak	— <i>Isca purpurea</i> , <i>Chimarra</i> T ₁ , <i>Simulium</i> T ₂
Night active with a dawn peak	— None
Night active with a dusk and dawn peak	— <i>Pseudocloeon</i> T ₁ , <i>Pseudocloeon</i> T ₂
Dawn and/or dusk peaks only	— <i>Indobaetis</i> sp., Orthoclaadiinae, Chironominae (larvae pupae), Ephemeroptera imagines

STATZNER et al. 1984; BENKE et al. 1986; BRITTAIN & EIKELAND 1988) although other patterns, including dusk or day-time (diurnal) drift, are known for some taxa (BRITTAIN & EIKELAND 1988). For example, some diel periodicity was apparent for 28 out of 33 taxa of insects drifting in Tai Po Kau Forest Stream (DUDGEON 1983d); 19 taxa drifted throughout the night, three were active at night with a dusk peak, two taxa were active at night with a dusk and dawn peak, while dawn and/or dusk peaks only were shown by a further four taxa (Table 8). None of the taxa investigated had higher drift rates during the daylight hours than at night.

While it is clear that changes in light intensity cause initiation and cessation of invertebrate drift (WATERS 1972; BRITTAIN & EIKELAND 1988), the underlying cause of diel drift periodicity, and in particular the nocturnal peaks in activity, is not clear. There is evidence that searching invertebrate predators – such as stoneflies – can induce up to 70% of the nightly baetid mayfly drift numbers (MALMQVIST & SjöSTRÖM 1987). Nocturnal drift may, in addition, be an evolutionary response to avoid visually-orientating predators such as fish (ALLAN 1978, 1984), and there are reports that drift is suppressed following introduction of fish to artificial streams (WILLIAMS & MOORE 1982) although the effect varies according to the nature of the local environment (WILLIAMS & MOORE 1989). The observation that large mayfly larvae tend to drift more at night (ALLAN 1978) has also been attributed to predator avoidance behaviour, as fish will tend to prey more upon large than small individuals and visual predators are impaired at night. One investigation providing strong support for the importance of predators in bringing about nocturnal drift, compared drift in a stream lacking fish with one adjacent where fish had been introduced 25 years earlier (MALMQVIST 1988). Nocturnal peaks in baetid mayfly drift were apparent only in the stream with fish; drift was aperiodic in the absence of fish. In addition, mayflies drifting at night in the stream with fish were larger than those drifting during the day (MALMQVIST 1988).

Although the tendency for large larvae to drift at night has some generality among geographically-distinct streams with different vertebrate predator-mayfly prey combinations (ALLAN 1978), there is no body size-drift relationship among chironomid (Diptera) larvae (SKINNER 1985). If predation is a selective force acting on invertebrate behaviour, we would expect similar patterns of drift to be exhibited by chironomids and mayflies. That this is not the case seems to cast doubt on the role of predation as a general causative mechanism, although it may be important for mayflies and especially Baetidae.

Periodic behaviour of animals on the stream bed may stimulate peaks in drifting activity. Two types of behavioural periodicity have been identified: diel positioning changes (changes in density on the top of the substratum) and diel variations in activity levels (WILEY & KOHLER 1984). Diel drift periodicity may be due to accidental dislodgement or active release of animals from the stream bed and, if the departure mechanism is entirely passive, we would expect drift rates to be related to diel changes in the density and activity of animals on the upper surface of the stream bed. By contrast, if density on upper substrate surfaces and in the drift do not correspond, then active mechanisms must be operating (RADER & WARD 1990).

A range of mayfly taxa are present in higher densities on the top of stream substrata at night, but drift rates are not necessarily correlated with these nocturnal increases in density (CASEY 1987). In fact, there is no obvious elevation in drift rates during periods of higher substrate surface densities of mayfly larvae (STATZNER &

MOGEL 1985), and no clear relationship between stone-surface densities and drift has been established (KÖHLER 1983; GRAESSER & LAKE 1984; ALLAN et al. 1986). There is also considerable doubt as to whether drift is related to changes in benthic activity levels in any simple fashion (CORKUM 1978a; ALLAN et al. 1986). Further site-specific considerations complicate the issue further: RADER & WARD (1990) record that a diel shift in benthic substrate utilization corresponding to drift periodicity in *Baetis* larvae occurred only in a stream above a deep-release reservoir, and did not take place at sites downstream of the reservoir.

While activity levels or population densities on stone surfaces may have an influence on drift periodicity, the evidence for such a relationship is weak. A complete explanation of the diel drift patterns that occur in both tropical and temperate streams probably will have to include the influence of predatory fish and benthic invertebrate predators, as well as consideration of endogenous rhythms (ELLIOTT 1968). Hunger may also serve as a stimulus for the initiation of drift (WILLIAMS & LEVENS 1988). In addition, the behaviour of the animals while drifting must be understood more fully, because certain mayflies prolong drift actively at night but leave the drift quickly during the day (CAMPBELL 1985). Together, these processes contribute to the complex array of factors that result in the diel periodicity of drift.

Seasonal fluctuations

The downstream transport of invertebrates varies not only over the course of the day but also from season to season, and the intensity of diel periodicity may also change over the year (BENKE et al. 1986). In temperate regions, drift rates are usually lowest during the winter (BRITTAIN & EIKELAND 1988), but there are few data on this aspect from lotic habitats in the tropics. Drift in some subtropical streams peaks during the winter (COWELL & CAREW 1976), but in others drift densities remain relatively constant throughout the year (BENKE et al. 1986) and a rather similar pattern prevails in tropical streams (BISHOP 1973; J.D. HYNES 1975b). A seasonally-constant drift rate need not, however, imply stability in the taxonomic composition of the drift (BENKE et al. 1986), although the causes of such temporal changes (life-history events or environmental cues) are obscure.

There are marked spring and autumn peaks in drift densities (numbers of animals per unit volume of water) in Tai Po Kau Forest Stream (Fig. 20). Over 100 taxa have been recovered from the drift during a 12-month period, and the number of taxa drifting – but not drift density – is positively related to water temperature (DUDGEON 1990b). Baetid mayflies dominate the drift, comprising approximately 40% of all drifting animals, and are over-represented relative to their contribution to total benthic standing stock. However, the importance of baetids in Tai Po Kau Forest Stream drift is in general agreement with accounts of drift composition in small streams in other regions, and the observation that a few abundant taxa constitute a high proportion of the drift seems typical (e.g. COWELL & CAREW 1976).

Data on individual insect taxa in Tai Po Kau Forest Stream reveal a variety of patterns of drift seasonality (DUDGEON 1990b). Blackfly larvae (Diptera: Simuliidae) are most numerous during the cooler months (November – March), and drift densities correlate negatively with water temperature (Fig. 21). Drift of two species

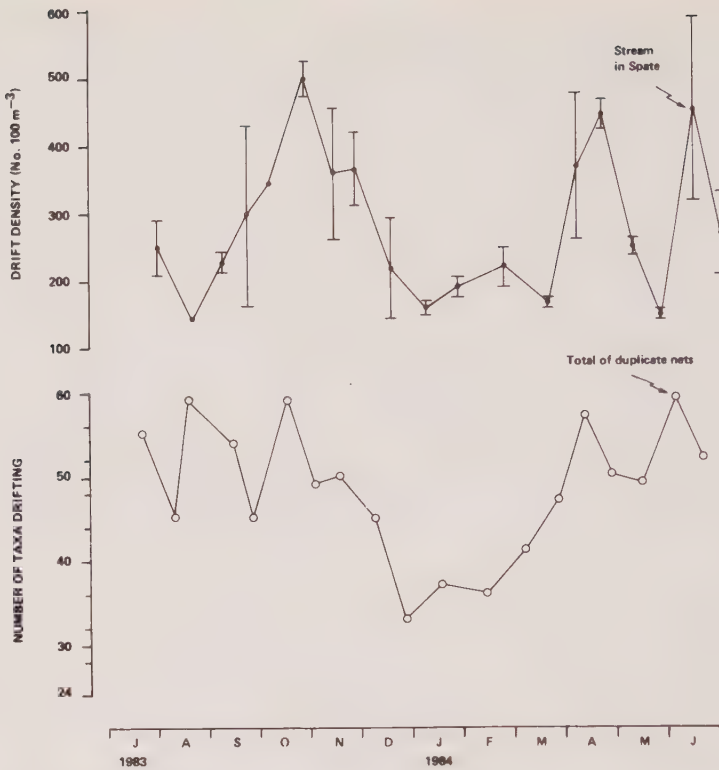


Fig. 20. Seasonal variations in the number of taxa drifting and drift densities in Tai Po Kau Forest Stream (1983–84).

of Baetidae peak in autumn (September – November), a third species is most numerous in autumn and spring (Fig. 21), while *Indobaetis* sp. drift densities are highest in spring (March and April). Two other non-baetid mayflies show spring peaks in drift, but there are no significant relationships between water temperature and the drift densities of any mayfly species. Both positive and negative responses of drift densities to water temperature (associated with summer and winter drift peaks respectively) have been recorded among Trichoptera species, and the only stonefly to drift in any numbers (*Amphinemura chui*; Nemouridae) is significantly more abundant in the winter months (Fig. 21).

Changing water temperatures (rising or falling) may trigger drifting behaviour in some species, but other factors, such as photoperiod (e.g. shorter summer nights) or phases of the moon (J.D. HYNES 1975b), can influence drift seasonality. It is notable that drift densities in Hong Kong species with summer or winter (and not spring and/or autumn) peaks are significantly related to water temperature, but that the effects of changing temperature varies between taxa. Drift of the caddisflies *Polymorphanisus astictus* (Hydropsychidae) and *Anisocentropus maculatus* (Calamoceratidae), which show summer and winter peaks respectively, comprises mainly

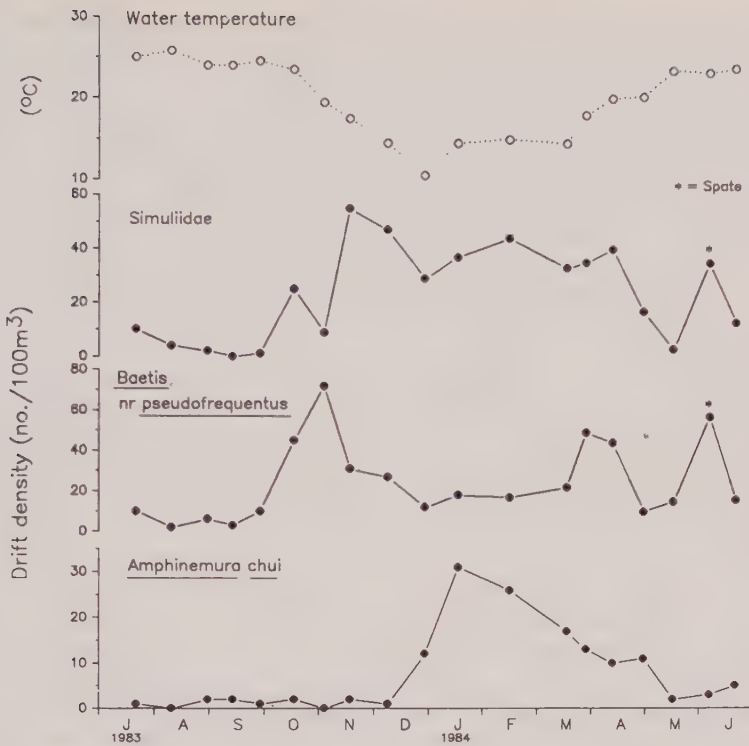


Fig. 21. Seasonal changes in water temperature and drift densities of simuliid (Diptera) larvae, *Baetis* nr *pseudofrequentus* (Ephemeroptera: Baetidae) and *Amphinemura chui* (Plecoptera: Nemouridae) in Tai Po Kau Forest Stream (1983–84).

first-instar larvae and is associated with recruitment. Drift of other taxa involves a range of instars and cannot be linked with known periods of oviposition or adult emergence.

Our understanding of the causes of diel variations in drift rate is limited; accordingly, our ability to explain longer-term fluctuations and drift seasonality is restricted. Environmental changes must play a role in initiating drift, because diel and seasonal variations in drift are notably small in streams with constant temperature and discharge regimes (ALLAN *et al.* 1988). Life-history events will also influence drift seasonality (CLOUD & STEWART 1974), as in certain Hong Kong caddisflies, but we should not expect control mechanisms to be identical for all species, nor even among species within the same family or order.

Population implications of drift

Drift has obvious importance as a mechanism of dispersal, and aids in the colonization or recolonization of denuded patches of substrate in permanent streams (BENSON & PEARSON 1987a; BRITTAIN & EIKELAND 1988). Drift can also be

used as a means to avoid unfavourable areas, and data from Hong Kong and elsewhere show that rheophilic animals have a greater tendency to drift out of pools than from riffles (KOVALAK 1978; DUDGEON 1983b).

Although drift can serve as a means of locomotion between suitable microhabitats in streams and rivers, the fact that large numbers of invertebrates drift has led to the idea that headwater regions would be denuded unless upstream movement occurred. Upstream movements by animals crawling along the stream bed do not generally compensate for rates of drift, so that insect-dominated lotic faunas show a net downstream displacement (BENSON & PEARSON 1987b; SÖDERSTRÖM 1987; BERGEY & WARD 1989). Compensatory movement could take the form of upstream flights by female imagoes (MÜLLER 1982), but the evidence for this is equivocal (NISHIMURA 1981; DUDGEON 1988b; JONES & RESH 1988). Downstream loss of individuals is only significant for the dynamics of lotic populations if oviposition and production rates are limited in upstream reaches. Present evidence indicates that despite substantial downstream losses (ELLIOTT 1981), production and oviposition rates in many streams are sufficient to provide for the observed drift without the necessity of compensatory upstream migration (WATERS 1981; WILZBACH & CUMMINS 1989).

Downstream export of stream animals in the drift will not require any compensatory upstream movement if such drift is production in excess of carrying capacity (WATERS 1961, 1972). The evidence for density-dependent drift (i.e. higher drift rates from denser populations) is inconclusive (CORKUM 1978b; STATZNER & MOGEL 1985; STATZNER *et al.* 1987; BRITTAIN & EIKELAND 1988), and both density-dependent and density-independent drift has been recorded, sometimes for the same species on different substrata or at different current velocities (BRITTAIN & EIKELAND 1988; WILLIAMS & MOORE 1989). The clearest evidence of density-dependent drift comes from investigations of territorial species which contest ownership of feeding areas (HART 1987a); in many cases, the defeated larvae swim up into the water column and so become part of the drift (HILDREW & TOWNSEND 1980).

If some drift is a result of contest competition or production in excess of carrying capacity, it is reasonable to assume that drifting animals are in poorer condition than non-drifters (MINSHALL & PETERSEN 1985) or suffer from pathogenic infestations (CUMMINS & WILZBACH 1988). Such differences would be disclosed by comparing of a sample of each group. One such investigation has shown that mortality of drifting animals held without food from 12 hours after collection was three times that of non-drifting (benthic) individuals (WILZBACH & CUMMINS 1989). An increased frequency of injuries (missing or damaged limbs) in drifting animals, which may result from encounters with predatory invertebrates, has also been recorded (WILLIAMS & LEVENS 1988), and wounded individuals may be more easily swept up into the drift than animals with a full complement of legs.

While the data are not conclusive, one role of drift seems to be removal of the 'doomed surplus' of individuals from benthic populations. Drift may not, therefore, regulate populations in a density-dependent way around a carrying capacity set by the habitat; instead, drift is merely the vehicle by which organisms are removed (WILZBACH & CUMMINS 1989). Population densities may be regulated by predation or pathogens (CUMMINS & WILZBACH 1988), or determined by density-independent agencies such as physico-chemical extremes or crushing and scouring during spates,

with drift merely carrying downstream individuals eliminated from the population by limiting processes.

While drift remains a puzzling phenomenon, we can infer that under some circumstances this behaviour is an expression of population-control mechanisms. At other times, drift densities reflect life-cycle events, especially larval recruitment. Temperature changes may serve as proximal stimuli for drift in some Hong Kong species, but the ultimate selective pressures causing drift seasonality remain unclear.

Interspecific competition and niche dimensions

The idea that there is a limit to the similarity of two species' niches has led to investigations of how animals partition resources in nature. Such partitioning commonly occurs along the ranked axes of habitat > food > temporal dimension, although habitat is less often the more important dimension for aquatic animals (SCHOENER 1974). The observed patterns might result from the influence of competition upon community structure (e.g. MOYLE & SENANAYAKE 1984; MOYLE & VONDRACEK 1985 and reviews by CONNELL 1983; SCHOENER 1983), but this may not be the only process at work (JEFFRIES & LAWTON 1984, 1985; FULLER & HYNES 1987).

It is noteworthy that field studies on groups of ecologically-similar species have usually revealed a partitioning of resources (TOWNSEND & HILDREW 1979), and species not segregated by habitat tend to show low dietary overlap (MOYLE & SENANAYAKE 1984). If interspecific interactions such as competition are important determinants of the size of populations of stream animals, then we should expect niche dimensions to display evidence of segregation. Such data are available for four species of Odonata and four benthic fishes in Tai Po Kau Forest Stream.

Odonata

Larval Odonata are generalist predators exhibiting little dietary selection (PRITCHARD 1964; THOMPSON 1978a; DUDGEON & WAT 1986), although there may be a failure to consume some taxa of potential prey (LAWTON 1970; KOSLUCHER & MINSHALL 1973; JOHNSON 1982). Studies of co-occurring Odonata have demonstrated both significant interspecific dietary overlap (MERRILL & JOHNSON 1984) and dietary partitioning (CARCHINI & NICOLAI 1984; BLOIS 1985). Size differences among species within seasons may reduce dietary overlap (KORMONDY & GOWER 1965; JOHANSSON 1978; CROWLEY & JOHNSON 1982a), because large larvae tend to have a more varied diet than smaller ones (PRITCHARD 1964; LAWTON 1970; THOMPSON 1978b; BLOIS 1985; DUDGEON & WAT 1986; DUDGEON 1989b). Such size differences generally arise from temporally offset life cycles (CROWLEY & JOHNSON 1982a), and this partitioning could be viewed as seasonal segregation (*sensu* SCHOENER 1974) which may reduce interspecific competition (BENKE & BENKE 1975).

Competitive exclusion seems to be rare among Odonata (CROWLEY & JOHNSON 1982b), where larval habitat and seasonality are important axes of resource partitioning (CROWLEY & JOHNSON 1982a). Life-cycle similarity among Tai Po Kau Forest Stream Odonata (DUDGEON & WAT 1986; DUDGEON 1989b, 1989e) greatly

reduces the potential for temporal separation of niche dimensions. Among these Odonata, the damselfly *Euphaea decorata* (Euphaeidae) has the broadest niche axes along both the food and habitat dimension, whereas the dragonfly *Zygonyx iris* (Libellulidae) is a relative specialist. However, the four commonest species in the stream make rather similar use of microhabitats, and regression models predicting the population densities of *E. decorata* and the dragonflies *Heliogomphus scorio* and *Onychogomphus sinicus* (Gomphidae) include similar substrate statistics as independent (predictor) variables (DUDGEON 1989c).

The role of sediment characteristics in determining gomphid microdistribution is not unexpected, as *O. sinicus* is a burrowing species, and data from other regions point to the importance of sediment characteristics – particularly grain size (KEETCH & MORAN 1966; HUGGINS & DuBOIS 1982) – in habitat selection. *Heliogomphus scorio* does not burrow, but sprawls among accumulations of allochthonous detritus where it is rendered cryptic by its colour. *Euphaea decorata* occurs amongst and under stones, as does *E. ochracea* in Malaysia (FURTADO 1969; BISHOP 1973). *Zygonyx iris*, by contrast, clings to the exposed surfaces of rocks and boulders in swift current, and is morphologically adapted to this habit (DUDGEON & WAT 1986). Such observations demonstrate that, even within patches, some spatial partitioning of the stream habitat by Odonata is possible. Clearly, estimation of the importance of habitat as a dimension of niche segregation will be strongly influenced by the scale of observation, because it is this which determines our ability to discriminate microenvironmental factors of relevance to a rather sedentary odonate.

If there is a limiting similarity to the niches of Tai Po Kau Forest Stream Odonata, segregation could occur along the food dimension. The extent to which the limited spatial partitioning among the study species might have affected the types of prey encountered is unclear, but it is noteworthy that the occupation of an extreme microhabitat by *Z. iris* results in a relatively specialized diet which includes typically rheophilic taxa (simuliid larvae and mayfly genera such as *Baetiella*, *Pseudocloeon* and *Epeorus*) (DUDGEON 1989c; DUDGEON & WAT 1986).

Interspecific dietary overlap is greatest between the two gomphids, and relatively low among other species pairs. If there are correlations between odonate labium morphology (i.e. the form of the prey-catching apparatus) and biological characteristics of the prey (PRITCHARD 1964), then similarity of labium morphology among related species may account for the high interspecific overlap in gomphid diets. This hypothesis seems to conflict with our knowledge of the difference in habits between the two gomphids (sprawling versus burrowing) which could have affected their foraging. Contrasting foraging strategies can lead to dietary differences among predators, even those which are not habitat specialists (TOWNSEND & HILDREW 1979; DUDGEON & RICHARDSON 1988). The lack of such an effect – and the similarity of gomphid diets – indicates that the subset of 'catchable' invertebrates from among the benthic community does not differ greatly, regardless of whether the predator employs the labium while sprawled on the substratum or while buried in the sediment.

Overlaps in diet and hence a reduction in possible competition between *H. scorio* and *O. sinicus* could have been reduced by temporal segregation (BENKE & BENKE 1975; CROWLEY & JOHNSON 1982a; WISSINGER 1988). Although these two species have similar life cycles, larval development within each population is asynchronous

(DUDGEON 1988e). Such intraspecific asynchrony yields a broad range of body sizes within both species throughout most of the year and, since different-sized larvae have somewhat dissimilar diets (to a greater degree in *H. scorpio* than *O. sinicus*), this could reduce the intensity of any competition for food (CROWLEY & JOHNSON 1982a; CROWLEY et al. 1987; WISSINGER 1988). Indeed, intraspecific overlap within both species was slightly less than interspecific dietary overlap between comparably-sized larvae (DUDGEON 1989e). Note that there will be a trade-off between competition and predation which will affect the efficiency of size segregation as a means of niche partitioning. As the difference in size between co-occurring larvae increases, the possibility of interspecific predation or cannibalism will also rise (WISSINGER 1988). Intraspecific size variability will therefore create the potential for mixed competition-predation interactions within and between populations.

While there is some partitioning of food among the Tai Po Kau Forest Stream Odonata, as well as probable microhabitat partitioning on a fine scale, interspecific segregation along the spatial and dietary niche axes of co-occurring Gomphidae appears minor. It seems unlikely that interspecific competition plays a significant role in determining the structure of this odonate assemblage. Such partitioning as is observed may result from phylogenetic constraints of morphology on the microhabitat preferences and foraging strategies of the three families concerned.

Fishes

Four species of benthic fishes are common in Tai Po Kau Forest Stream and widespread among unpolluted hillstreams in Hong Kong. They are *Pseudogastromyzon myersi* and *Liniparhomaloptera dispar* (Homalopteridae or Balitoridae; KOTTELAT 1988), the goby *Tukugobius wui*, and *Noemacheilus fasciolatus* which has long been placed in the Cobitidae (the loaches) although some suggest it should be included among the homalopterids (SAWADA 1982). All four species inhabit rocky-bottomed riffles and pools, and are thus potentially interacting populations.

Recent literature pertaining to niche segregation in lotic fishes indicates that both microhabitat utilization and diet can be important dimensions of resource subdivision (e.g. GEORGE & HADLEY 1979; MIZUNO et al. 1979; MATTHEWS et al. 1982; PAINE et al. 1982; SURAT et al. 1982; WYNES & WISSING 1982; WELTON et al. 1983; MOYLE & SENANAYAKE 1984; SCHUT et al. 1984; WIKRAMANAYAKE & MOYLE 1989), and it is noteworthy that species not segregated by microhabitat tend to show low dietary overlaps (MOYLE & SENANAYAKE 1984; WIKRAMANAYAKE & MOYLE 1989). These findings can be viewed as support for the contention that fish populations (and hence community structure) in tropical running waters are influenced strongly by competition (ZARET & RAND 1971; MOYLE & SENANAYAKE 1984; WATSON & BALON 1984; LOWE-McCONNELL 1987; WIKRAMANAYAKE & MOYLE 1989). By contrast, other studies in the tropics have shown a great deal of overlap in the resource use of coexisting fish species (COSTA & FERNANDO 1967; KNÖPPEL 1970; BISHOP 1973; GOULDING et al. 1988).

The benthic fishes of Tai Po Kau Forest Stream exhibit niche overlaps along both the dietary and microhabitat dimensions (DUDGEON 1987b). Although there is broad dietary separation between the homalopterids *P. myersi* and *L. dispar* which consume periphytic algae and fine detritus – when compared with predatory *N. fasciolatus* and *T. wui*, there is extensive overlap between species pairs in each feeding

guild. There are some minor differences in the microhabitat utilization and substrate preferences of *L. dispar* and *P. myersi*, but both species are associated with rocks and stones in midstream microhabitats where they graze periphyton. Some microhabitat segregation has been reported among sympatric Malaysian homalopterids (ALFRED 1969), although three of these fishes were nevertheless described as rock-dwelling species. However, there is no clear evidence of microhabitat partitioning among Tai Po Kau Forest Stream homalopterids, despite the similarity of their diets.

A degree of microhabitat segregation occurs between the homalopterids and predatory *T. wui* and *N. fasciolatus* with the latter two species occurring closer to the banks than the homalopterids (DUDGEON 1987b). Although microhabitat utilization can be an important dimension of niche segregation in certain cases, avoidance of competition clearly cannot be invoked as the cause of differences in the microhabitat preferences of predatory and algivorous fishes. Indeed, the morphology of homalopterids – flattened body, modified pectoral and pelvic fins – would tend to restrict them to rocky or boulder-strewn habitats. An obligatory association with hard surfaces is apparent from examination of the feeding apparatus of *P. myersi*. Epilithic algae are detached from the substrate by a rasping action of the distal edges of the jaw which are coated with horny scales. These fish create a water flow through the gills by alternately expanding and contracting the mouth cavity, and thus suspended food particles collect on the gill rakers (HORA 1932; ARENS 1989). Microhabitat utilization by homalopterids would therefore arise from a morphological match of the fish with the habitat template, and here phylogeny rather than competition determines niche occupancy.

Tukugobius wui and *N. fasciolatus* are morphologically less specialized than either homalopterid species, and occupy a wider range of microhabitats and substrate types in Tai Po Kau Forest Stream. Again, however, there is considerable overlap in microhabitat use, although *N. fasciolatus* will forage in patches of allochthonous detritus which the goby tends to avoid. Notwithstanding, the similarity between the diets of these fishes is striking, and both feed extensively on chironomids and mayflies (especially Baetidae). The mechanisms of prey selection by these fishes has not been studied, but it is apparent that the diet includes only a subset of the range of benthic taxa in the stream, and those that are eaten constitute a major component of Tai Po Kau Forest Stream drift.

Niche segregation may be subtle, with (for example) the food habits of sympatric fishes differing only during periods of resource depression (GILLEN & HART 1980). Nevertheless, some studies have indicated either no dietary separation (BALTZ et al. 1982; PAPPANTONIOU & DALE 1982), or considerable overlap in prey size and taxa (MATHUR 1977; SCHLOSSER & TOTI 1984). While these observations might be explained away by invoking the hypothesis that stream fishes are habitat – not dietary specialists (GORMAN & KARR 1978; GATZ 1979), such is clearly not the case in Tai Po Kau Forest Stream where fishes with similar diets overlap more in microhabitat utilization than do fishes with dissimilar diets. The lack of resource partitioning indicates that interspecific competition has not been an important force shaping the population dynamics or evolution of these fishes.

Is competition important in Hong Kong streams?

The importance of competition in nature can best be investigated by field experiments but, under many circumstances, such manipulations are impractical. Another approach is to look for evidence of niche segregation among sympatric species, and to infer the action of competition from differences in diet, habitat use, and so on. This practice is based on the assumption that competition is a 'bad thing' for the species involved, and that natural selection will produce niche shifts which reduce the common exploitation of a limiting resource. There are, however, difficulties with this approach which are exemplified by the Hong Kong data. For example, although there is some meagre evidence of niche segregation by Tai Po Kau Forest Stream Odonata, the observed patterns indicate nothing of causal mechanisms. Although they may reflect the action of competition, this mechanism will only affect individuals and populations in conditions where resources are limiting and depletable. The matter is further complicated by the observation that competition among predatory stream insects may be an intermittent process with seasonal variations in intensity (BRUNS & MINSHALL 1986).

It is not known whether prey are limiting for Odonata in Tai Po Kau Forest Stream, but the small meal size (i.e. the low number of prey items per gut) and high frequency of empty guts among these predators (DUDGEON 1989c) might be indicative of food shortage. One estimate of the ability of a predator to deplete prey populations indicated that the gomphid, *Lanthus vernalis*, which comprised almost 27% of the invertebrate biomass in a North Carolina stream, had a modest impact on other invertebrates (WALLACE et al. 1987). This effect (or lack of it) was due to the rapid rate of prey turnover compared with that of odonate predators, and is in accordance with a general lack of strong evidence of predator effects on stream benthos community structure (ALLAN 1983). Such findings suggest that lotic Odonata are unlikely to deplete their prey significantly, a conclusion that is supported by the low rates of odonate production (1.02 g dry weight/m²/year for the four species combined) in Tai Po Kau Forest Stream (DUDGEON 1989e).

Data revealing extensive overlap in the niches of benthic fishes in Tai Po Kau Forest Stream do not concord with the hypothesis that competition has a significant influence on population dynamics in this habitat. A lack of interspecific dietary segregation within feeding guilds could result from a superabundance of food, although high fish population densities (5.7 individuals/m²) suggest that this explanation is unlikely to be correct. A further possibility is that fish population sizes are a reflection of seasonal disturbances of the environment. Unlike Odonata, which spend part of their lives in a terrestrial phase, fish cannot avoid spates resulting from typhoons and monsoonal rains. Such periodic catastrophes may cause density-independent mortality, so reducing the importance of competition and contributing to a lack of structure in fish assemblages (GROSSMAN et al. 1982). The importance of spates as determinants of odonate abundance is less clear as most adult emergence precedes the onset of the monsoon, but typhoons late in the season may cause flash-floods and catastrophic drift.

Available data indicate that the niche dimensions and population characteristics of lotic fishes and Odonata are not influenced strongly by interspecific competition. Correspondence in niche occupancy by species pairs of homalopterids or gomphids reflects a resemblance in general body plan and therefore some similarity in patterns

of resource acquisition. Furthermore, periodic spates in Hong Kong streams may keep population densities far below the carrying capacity of the habitat, and beneath the threshold at which competition for scarce resources will occur.

Biotic versus abiotic influences on lotic populations

The question "Is competition important in Hong Kong streams?" is germane to the wider enquiry by ecologists into the relative roles of physical disturbances (defined as any physical process removing residents from the population) versus biological interactions (including competition) as determinants of population size and as organizing forces in communities. It is likely that all streams are disturbed to some degree (DIAMOND & REICE 1985; REICE 1985; STATZNER 1987). The normal condition of benthic populations might be a state of recovery from the last flood or drought (REICE 1985), although recolonization of denuded patches following small-scale disturbance is rapid (LAKE *et al.* 1989). Unfortunately, little is known of the effects of disturbance at a large enough scale (*i.e.* involving the whole stream) to match that operating in nature (FISHER 1987). The picture is complicated further by the fact that opportunities for recolonization and population growth will depend upon the life cycles of the animals concerned, and thus outcome of disturbance will vary seasonally (ROBINSON & MINSHALL 1986).

While not all workers agree on the importance of disturbance, some believe that abiotic factors and seasonal processes are more important than biological interactions in determining population and community parameters (DIAMOND & REICE 1985). Moreover, the effects of floods and other disturbances might imply that biotic interactions are facultative rather than obligate, if indeed they are significant at all. A direct role of biotic interactions has, however, been established in some studies which have shown that predatory invertebrates and fish can influence prey distribution and abundance in streams (PECKARSKY 1979, 1985; PECKARSKY & DODSON 1980; GILLIAM *et al.* 1989; SCHLOSSER & EBEL 1989), and others demonstrating evidence of inter- and intraspecific competition between herbivores grazing algae on the tops of stones (HART 1981, 1987a, 1987b; LAMBERTI & RESH 1983; McAULIFFE 1984; HAWKINS & FURNISH 1987; LAMBERTI *et al.* 1987). By contrast, some investigations of predation have given rise to more equivocal results (ALLAN 1983; FLECKER 1984; FLECKER & ALLAN 1984; WALDE & DAVIES 1984; DUDGEON 1991a), and the outcome of a particular predator-prey interaction can change according to habitat conditions (WALDE 1986) with disturbances overriding the effects of predation (PECKARSKY 1985).

There is a developing consensus that highly variable and/or unpredictable flow regimes in streams provide a physical template where abiotic processes are of primary importance in determining population dynamics, whereas more benign or predictable flow environments are conducive to the development of stronger biotic interactions such as competition and predation (LAKE & BARMUTA 1986; HILDREW & TOWNSEND 1987; STATZNER 1987; POWER *et al.* 1988; RESH *et al.* 1988; POFF & WARD 1989). In most running waters, streamflow regimes are intermediate between these extremes or, as in Hong Kong, oscillate between them on a seasonal basis, with the consequence that both biotic and abiotic factors influence benthic populations at various times (ROBINSON & MINSHALL 1986; MINSHALL 1988). Each

species will vary in their responses to these factors due to the differences in physiology, morphology and behaviour imposed on them by their evolutionary history. The individualistic response of species to this diversity of physical and biological processes give rise to a particular assemblage of populations, scaling up ultimately to produce the community structure characteristic of a particular stream habitat.

III Individuals

Adaptation and optimal animals

All organisms are products of natural selection. In a sense, their environment acts as a filter: only those individuals with appropriate morphologies, physiologies or behaviours can survive and breed. They leave descendants which share the characters – adaptations – which made their ancestors successful. Clearly then, organisms are not *adapted to* their current environment, but *abapted from* ancestral environments.

Regardless of the nature of an adaptation, because of the environmental ‘filtering’ effect there is a match between local conditions and the type of organisms found there. Thus the inhabitants of a slow-flowing lowland stream differ from those of a mountain torrent (indeed such observations have prompted schemes of river zonation and classification), and denizens of two such torrents in separate mountain ranges possess analogous adaptations. For the same reason, animals in stony streams the world over manifest similar (but not identical) adaptations and habits (HYNES 1970).

While there can be no doubt of the occurrence and importance of adaptations in nature, some caveats must be introduced. It is senseless to examine all features of an organism and expect that every one have adaptive value, and it is equally pointless to persist in asking whether one adaptation is better than another (these points are elaborated further by GOULD & LEWONTIN [1979] and CALOW [1983]). Additional difficulties arise if we assume that all variation between individuals is inherited and, by inference, potentially adaptive. Some variation is a result of phenotypic plasticity, and the expression of this plasticity is lost with the death of the organism. For example, intraspecific variation in the shell shape of tropical and temperate freshwater snails can be affected by a variety of factors during development (e.g. BALAPARAMESWARA RAO & SUBBA RAO 1985; LAM & CALOW 1988), including water movement, but the shell shape that an adult finally acquires is not passed on to its offspring (ARTHUR 1982). The picture is complicated, however, by the view that phenotypic plasticity itself may be adaptive and under the control of natural selection (WAY & WISSING 1982; BAIRD et al. 1987; LAM & CALOW 1988; STEARNS 1989).

Natural selection (and hence adaptation) cannot be perfecting processes. For one reason, the features of an organism are not determined by prevailing conditions but by the interaction of foregoing generations with past environments. Secondly, because resources are limited, natural selection cannot perfect all of the features of an organism simultaneously. For example, the number of eggs that a mayfly produces cannot be increased at the same time that egg size (energetic investment per egg) is maximized. Thirdly, the development of a particular adaptation should

not be seen in isolation, but in the context of the organism as an integrated whole. Accordingly, maximizing egg production in a mayfly might be incompatible with adult flight ability, and aerodynamics will be traded-off against fecundity.

In essence, many attributes influence fitness, and it is not possible to maximize all fitness components simultaneously. There are trade-offs and constraints so that the fittest individuals optimize, rather than maximize, fitness components (TOWNSEND & CALOW 1981; SIBLY & CALOW 1986). Thus the appropriate trade-off between number and size of eggs will vary under different ecological circumstances, and the fittest individuals will allocate energy so as to achieve the optimal balance between these two parameters.

Consideration of natural selection as an optimizing process depends on a knowledge of the costs and benefits of possible adaptations in particular ecological circumstances; natural selection is assumed to have favoured the adaptation which maximizes the ratio of benefits to costs. For a mayfly living in an intermittent stream, the optimum balance between investment in eggs and in flight ability will be in the direction of increased dispersal. The cost of the extra weight of eggs will not be repaid in increased fitness if the insect cannot fly far enough to colonize a new stream. By contrast, a mayfly inhabiting a perennial stream will have less need to disperse and (all other things being equal) an increased investment in eggs will be repaid by greater fitness. High fecundity will therefore be traded-off against a loss in flying ability.

While it would be naïve to expect that optimality theory can be employed in a way that will permit us to understand all of the varied forms and behaviours exhibited by lotic animals, the approach does have explanatory and predictive power in some cases (KREBS & McCLEERY 1984). In addition, a failure of optimal solutions to match the adaptations of real animals can sometimes shed just as much light as a successful prediction on our understanding of their lives. For these reasons, the following discussion of the ecology of individuals will centre on adaptations linked, where possible, to predictions of optimality theory. Here it should be emphasized that our understanding of the population dynamics, and hence community structure, of lotic animals is dependent upon an appreciation of the interactions of individuals with the biotic and abiotic environment.

Feeding

Animals can be viewed as resource transformers, in that they ingest energy and nutrients in one form and transform them into soma, reproductive products or wastes. Individual fitness depends to a large degree on their success at this process, in particular the transformation of food into offspring. Foraging behaviour – the way in which animals acquire food and the choices they make while doing so – influences the amount, quality and types of food eaten and affects a variety of the life-history parameters of freshwater animals (ANDERSON & CUMMINS 1979; WARD & CUMMINS 1979; FULLER & MACKAY 1981; MARTIN & MACKAY 1983; HERRMANN 1984; SWEENEY & VANNOTE 1984; FULLER *et al.* 1988; ROSILLON 1988; SÖDERSTRÖM 1988). Optimal foraging behaviour will differ according to whether a consumer feeds on discrete food items, which may be dispersed widely in space and can occur at different densities – as is the case with animal prey – or whether the food is

widespread but does not occur as discrete items. In this instance the food may be in the form of a film – which is the situation faced by many primary consumers and grazers upon periphyton – or in more or less isolated patches. Such differences in resource characteristics require that foraging by primary and secondary consumers be considered separately.

Foraging behaviour: predators

Where foragers, especially predators, can estimate and act upon information about food availability in their surroundings, the evidence indicates that they attempt to maximize their net rate of energy gain (PYKE et al. 1977; COWIE & KREBS 1978; KREBS & MCCLEERY 1984; PYKE 1984). This makes good sense for an 'optimal animal', because fitness can be assumed to be an increasing function of the net rate of energy gain, and natural selection will favour individuals that can maximize this parameter.

Habitats can be viewed as divided into spatially separate areas or patches, each containing food although not necessarily in the same amounts. Optimal foraging theory attempts to predict the order in which these patches should be visited and the amount of time that will be spent feeding in each if the consumer is to maximize energy returns and minimize travelling or entry costs. In certain cases – where the patches are very small – they become equivalent to individual food items; optimal foraging theory can then be used to predict in what order food items should be consumed so as to maximize net energy gain, bearing in mind the costs of travelling as well as subduing and handling food items. On this basis, prey should be ranked and included in the diet in decreasing order of a measure of benefit derived from the prey divided by the costs of subduing and handling it.

Optimal foraging theory predicts that a consumer will exploit food items or patches which yield energy at a net rate above that for the items or patches in the habitat overall. In other words, a patch should be abandoned when the net rate of energy gain falls to a level equivalent to the average yield from all of the patches in the habitat. Similarly, a food item will be eaten when encountered if it will yield a higher than average net rate of energy gain, but if the rewards are lower than those obtained in the environment overall the food should be discarded. In essence, a patch is abandoned when the consumer would do better by feeding elsewhere; food is ignored or discarded if the consumer would do better by obtaining another item. These and other predictions of optimal foraging theory are discussed by PYKE et al. (1977), KREBS & MCCLEERY (1984) and PYKE (1984).

A simple application of optimal foraging theory involves its use in explaining dietary selection by a freshwater crab, in terms of the costs and benefits associated with different prey (DUDGEON & CHEUNG 1990). *Somanniathelphusa sinensis* (Parathelphusidae) occurs in lowland streams and rivers in Hong Kong, where a range of gastropod prey abound. Unlike many marine portunid crabs, which also consume molluscs (e.g. ELNER & HUGHES 1978; JUBB et al. 1983; DAVISON 1982), *S. sinensis* does not use its well-developed chelae to break open shells; instead the prey is grasped by the chelae and pieces are broken from the shell by the third maxillipeds. The cost to the crab of making a meal out of a snail will be the energy or time involved in breaking the shell. Accordingly, one currency for estimating the value

of a particular prey species to the crab would relate handling time (H , cost) to prey somatic dry mass (M , benefit). A predator maximizing its food intake should select items with the greatest M/H ; the highest reward in prey biomass per unit handling time. This benefit/cost construct is simple, but has been successful in predicting prey selection in molluscivorous cichlid fishes (SLOOTWEG 1987).

Prey offered to the crab included the heavy-shelled prosobranchs *Melanoides tuberculata* (Thiaridae) and *Sinotaia quadrata* (Viviparidae), as well as the thinner-shelled pulmonates *Biomphalaria straminea* (Planorbidae), *Physella acuta* (Physidae) and *Radix auricularia plicatula* (Lymnaeidae). Differing investment in defense among these snails is reflected in relative shell weights: *S. quadrata* has the highest shell weight: somatic weight ratio, *M. tuberculata* is second, with *R. auricularia plicatula*, *P. acuta* and *B. straminea* respectively third, fourth and fifth. If crabs are maximizing M/H then we might expect that *B. straminea* – with the thinnest shell – would be the preferred prey, *S. quadrata* being ignored until all of the other snail species are eaten. In fact, crabs are unable to break *S. quadrata* shells, and even the largest crabs can crack only small *M. tuberculata*. Actual measurements of M/H using large (two-year old) crabs yielded prey ranks (in descending value) of *B. straminea* > *P. acuta* > *R. auricularia plicatula* > *M. tuberculata*. Small (one-year old) crabs which cannot open *M. tuberculata* rank the pulmonates in the same order (DUDGEON & CHEUNG 1990).

If these freshwater crabs behave 'optimally', and if the M/H construct is useful, we would predict that when offered a mixture of snails the crabs would consume the most valuable species (*B. straminea*) preferentially. In fact, when offered a choice of the three pulmonate species, crabs do prefer *B. straminea* over *P. acuta*, and *P. acuta* over *R. auricularia plicatula* (DUDGEON & CHEUNG 1990). Moreover, small *B. straminea* are eaten before large ones. This is in agreement with the benefit/cost construct, because handling time rises exponentially as snail size increases – with a consequent decline in M/H – so that large snails are less-rewarding prey.

A straight-forward way of clarifying the importance of benefit/cost considerations to crabs choosing snail prey is to alter prey characteristics so as to increase handling time, and observe the crabs' response. Cementing a small plastic disc to one side of the planispiral shell of *B. straminea* effectively increases H without affecting M , thereby reducing prey value. When offered a choice, crabs prefer to eat unmodified snails rather than those with plastic discs attached (DUDGEON & CHEUNG 1990). *Somanniathelphusa sinensis* seems to choose prey in accordance with a simple optimality model that predicts that the predator will maximize net energy gain.

It is clear from this study that simple optimality models can help us to understand and predict aspects of the ecology of individual freshwater animals. Moreover, the behaviour of individual organisms can scale up to generate population or even community-level effects. *Somanniathelphusa sinensis* is common in the middle and lower course of the Lam Tsuen River where it coexists with the five species of snails used in the feeding trials. It is striking, however, that in localities where the crab is common, *S. quadrata* and *M. tuberculata* are the only abundant snails. Although the evidence is circumstantial, selection of thinned-shelled prey by the crab probably limits pulmonate densities. An effect of molluscivorous predators on the population dynamics of pond snails has been recorded elsewhere (BROWN & DEVRIES 1985; WEBER & LODGE 1990) and, in addition to some circumstantial evidence on the importance of such predators in structuring freshwater communities (LODGE et al.

1987), recent studies have indicated that fish and crayfish preying on grazing snails have a positive indirect effect on periphyton (BRÖNMARK 1990; WEBER & LODGE 1990).

A notable aspect of *S. sinensis* foraging is a tendency to abandon partially-eaten snails when additional prey are present (DUDGEON & CHEUNG 1990). Meals are always completed, by contrast, when snails are offered to the crabs singly. A similar rejection of partially eaten molluscs when prey are abundant has been recorded for marine portunid crabs (JUBB et al. 1983; DAVISON 1986).

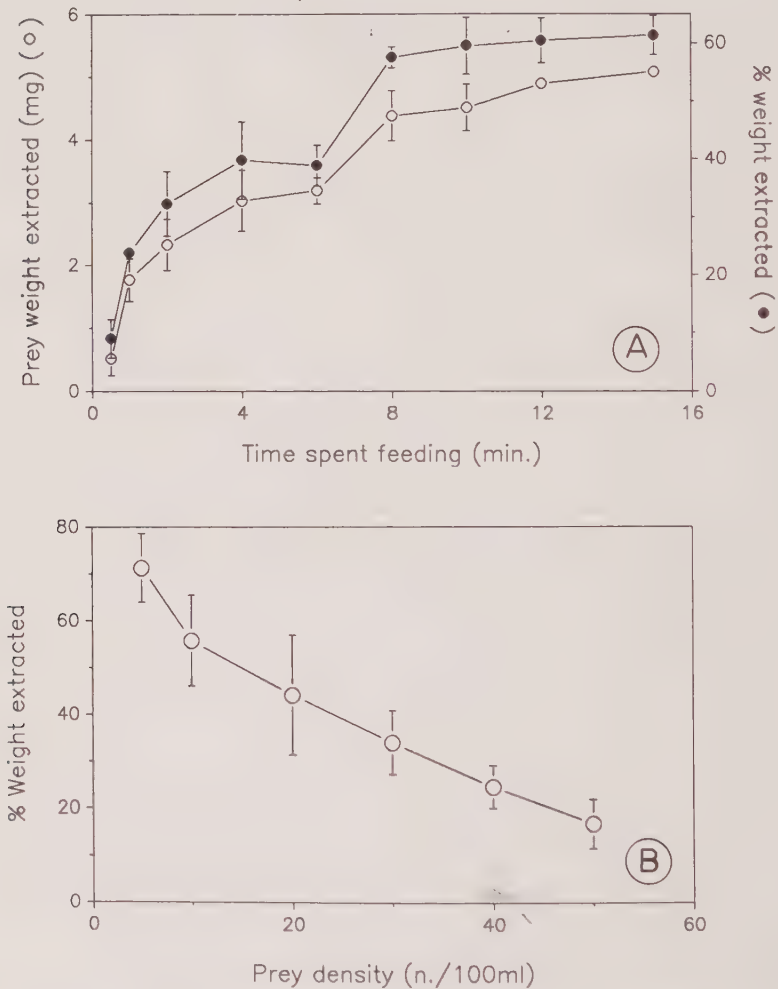


Fig. 22. The weight of food extracted (mean \pm 1 S.E.M.) from *Chironomus* prey during feeding by *Diplonychus rusticum*. The percentage of total extractable food that was removed is also shown. B: The relationship between prey density and the percentage of each prey consumed (wet weight extracted/initial weight \times 100%; mean \pm 1 S.E.M.).

Partial prey consumption has been observed in heteropteran (Insecta: Hemiptera) predators which treat each prey as if they were a resource patch (SIH 1980; BAILEY 1986) and spend considerable time handling each item. In such cases, rates of return from a single prey item decline as the time spent feeding on it increases, which is analogous to a decrease in patch quality as the amount of food remaining decreases. Predators can thus maximize energy intake at high prey densities by feeding for a short time on each prey item (COOK & COCKRELL 1978) and may abandon a meal while some extractable material still remains (SIH 1980; BAILEY 1986), providing that net energy intake rate can be increased by searching for and capturing more rewarding prey. On this basis, increasing prey availability (provided it decreases search costs) should reduce the time spent feeding on each item (SIH 1980) and result in partial consumption of prey. This is equivalent to one prediction of optimal foraging theory: that consumers should spend less time feeding per patch in more rewarding habitats (CHARNOV 1976). *Somaniathelphusa sinensis* practises partial prey consumption only when groups of snails are offered, and when search time is unlikely to contribute to prey selection. Such behaviour may be a result of crabs maximizing their net rate of food intake, and it is significant that crabs which eat part of the prey tear off pieces of snail flesh without resorting to shell breakage. This attack strategy allows a high initial rate of food gain, but necessitates considerable additional investment to obtain the remains of the prey deep within the shell. Where prey are abundant, attacking another snail may be more profitable than persisting with the original meal.

The belostomatid bug, *Diplonychus rusticum*, is one of the commonest heteropterans in Hong Kong freshwaters, and can be collected from among aquatic macrophytes or trailing vegetation along the banks of slow-flowing rivers and streams. These insects breathe atmospheric air, and so must return to the water surface periodically, but this characteristic allows *D. rusticum* to survive in polluted waters where dissolved oxygen levels may be quite low. Like most other predacious heteropterans, *D. rusticum* grasps prey in the raptorial forelegs and consumes the body contents by sucking. Belostomatids are highly polyphagous and will attack other insects as well as fish, tadpoles and snails (VENKATESAN & RAGHUNATHA RAO 1979; VICTOR & UGWOKÉ 1987; CLOAREC 1989; KESLER & MUNS 1989); in the laboratory, *D. rusticum* readily accepts chironomid larvae which are abundant in the predator's natural habitat.

Diplonychus rusticum is easy to maintain in captivity making it a convenient species for the examination of partial prey consumption. This species has been investigated to determine whether one assumption about patch use by heteropterans is correct: do returns from a prey item decline as the duration of feeding increases? Measurements of the change in weight of *Chironomus plumosus* (species-group) larvae during feeding bouts by *D. rusticum* show that the first two minutes of feeding permit the predator to obtain approximately 33% of the available food (Fig. 22A); feeding for 10 minutes results in only 60% extraction (DUDGEON 1990c).

The results indicate that, at high prey densities, a predator which partially consumes two prey in a total time of four minutes will do as well (in terms of weight of food extracted) as one feeding on a single chironomid for ten minutes.

With this information we can test if *D. rusticum* feeds optimally: does the predator reduce the proportion of each prey ingested in response to increases in prey density?

There are significant differences in the percentage of each chironomid prey eaten

at different prey densities (Fig. 22B), and at high densities only 17% of the body weight of each larva is extracted, increasing to 71% when prey are scarce. Evidently, the predators are more 'wasteful' and eat less of each prey as chironomid densities increase (DUDGEON 1990c). *Diplonychus rusticum* conforms to a simple optimal feeding model because, since the rate of food intake declines as a greater proportion of each prey is extracted (equivalent to time spent in a patch), food intake is maximized by partial consumption of each item as prey density increases. In other words, the richer the habitat, the shorter feeding time per patch. This finding is in agreement with other studies of feeding by aquatic Heteroptera (COOK & COCKRELL 1978; GILLER 1980; SIH 1980; BAILEY 1986).

As well as altering the duration of feeding as prey densities increase, *D. rusticum* and other belostomatids vary their foraging tactics according to circumstances, and may ambush prey or seek out quarry actively (CLOAREC 1989). In addition, these animals exhibit hoarding behaviour by capturing and retaining a second prey while feeding on another (VICTOR & WIGWE 1989). The predator holds onto the second prey until it has completed feeding on the first. Consumption of the second prey may be accompanied by hoarding a third victim.

The behavioural versatility of *D. rusticum* may have population-level implications, as exemplified by some data on feeding rates. Predators may be faced with an unpredictable food supply, and the consequences of reduced prey availability on *D. rusticum* have been investigated by comparing the life cycle of the bug under different feeding regimes. Individuals which were allowed to feed *ad libitum* every day passed through five larval instars to maturity in 53 days, 11 days earlier than those which were fed only every fourth day. These values are similar to development times for laboratory and field populations of the closely related Indian belostomatid *Sphaerodema annulatum* (VENKATESAN & RAGHUNATHA RAO 1979). *Diplonychus rusticum* larvae in the under-fed group spent approximately twice as long in the first instar, but the time spent in each of the second, third and fourth instars was only two days longer, and the duration of the fifth instar was similar in both groups (Fig. 23A). The ability of partially-starved *D. rusticum* to 'catch up' with well-fed animals was not at the expense of body weight, as mature bugs from the two feeding groups weighed 23.2 and 22.1 mg (dry weight) respectively. Instead, the effect reflected an adjustment of meal size, with under-fed *D. rusticum* larvae of instars II – V eating approximately four times more food on the days that they were fed than the daily food consumption of bugs under the *ad libitum* feeding regime. As a result, the overall daily food consumption per unit weight of predator was almost the same in both groups (Fig. 23B).

The feeding rates of first-instar *D. rusticum* larvae were particularly high, corresponding to a daily ingestion rate equivalent to the predators own body weight (Fig. 23C). The fact that partially-starved young bugs spent almost twice as long in the first instar may reflect an inability to process the amount of food (four times their body weight during a single day) needed to keep up with their well-fed counterparts. Physiological constraints during this instar may have limited behavioural flexibility as a means of coping with periodic food shortages.

While *D. rusticum* larvae cannot increase feeding rates enough to compensate completely for periods of starvation, an ability to adjust behaviour to compensate for changes in local circumstances emphasizes the importance of considering the ecology of individual animals when there is a need to explain population- or

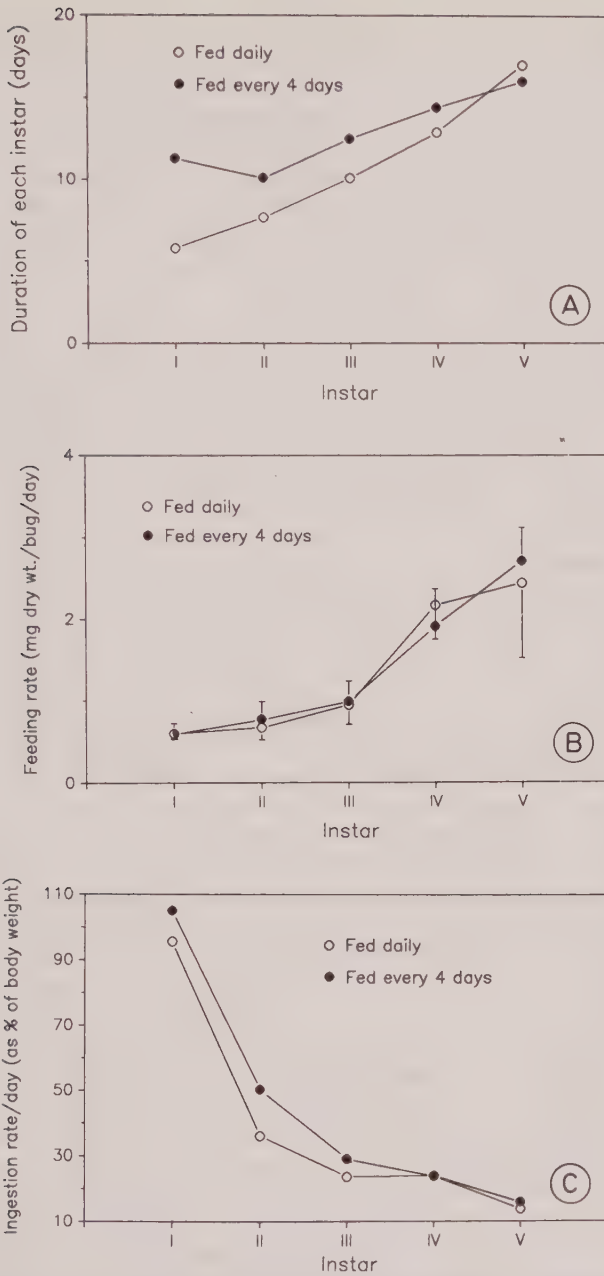


Fig. 23. A: The duration of larval instars in groups of *Diplonychus rusticum* fed daily or fed once every four days. B: Rate of food consumption (in terms of weight of food eaten per bug per day) by different larval instars of *Diplonychus rusticum* under two feeding regimes. C: Rate of food consumption, expressed as a percentage of predator body weight, by different larval instars of *Diplonychus rusticum* under two feeding regimes.

community-level phenomena in freshwater habitats. The results that arise from studies of this bug and freshwater crabs feeding on snails indicate that individuals adjust their foraging modes on the basis of economic considerations. This versatility confers a degree of individualism upon each member of a population, with the implication that explanation of population-level phenomena may not come from viewing all members of that population as identical automata (HOUSTON et al. 1988). Individual flexibility will need to be taken into account if we are to understand fully the ecology of the running-water fauna.

Foraging behaviour: primary consumers

The versatility of predator foraging strategies may not seem surprising as we are used to the idea that predators must be fleet of foot, cunning, or in some way superior to the animals upon which they prey. But what of primary consumers, which feed on algae or detritus? Their food is sedentary and often blankets the sediments of streams and rivers. Do primary consumers exhibit any of the behavioural versatility and individualism shown by foraging predators?

Comparative studies of foraging by stream fauna are scarce, and little is known of the key evolutionary pressures that these animals face while searching for food. In addition, we need a better understanding of relative resource levels, and the scale and magnitude of patchiness in stream (WILEY & KOHLER 1984). As it is, we do not know whether food is often in short supply in streams, nor whether resource competition is rare or common. Neither do we know if these questions have the same answers for primary and secondary consumers. Nevertheless, there is no *a priori* reason why primary consumers should not maximize their net rate of energy intake, since this parameter is just as likely to be correlated with fitness in primary consumers as it is in predators.

Non-random feeding patterns of macrophagous predators can be investigated relatively easily, but primary consumers in running waters may be ingesting tiny algal cells and fine particulate organic material. Under such circumstances, it is difficult to determine whether a microphagous consumer is feeding selectively or eating items in the same proportions as they are encountered. This difficulty is magnified by the generalization that some lotic primary consumers, such as pulmonate snails, are grazers which use their radulae to scrape a variety of food materials from suitable surfaces (RUSSELL-HUNTER 1978). Although some snails are selective, preferentially ingesting detritus or even bacteria rather than algae (CALOW 1973, 1974), and food choice may influence their distribution (LODGE 1986) or egg production (SKOOG 1978), methodological problems have retarded progress towards our understanding of optimal diet choice by microphagous primary consumers.

An alternative approach to investigating optimal diets involves consideration of movement patterns during foraging. Just as the optimal diet involves non-random selection of food items, so must movement during foraging be non-random if only to ensure that the consumer does not re-visit a patch which it has depleted recently. Such foraging movements have been investigated using seven species of freshwater snail from the Lam Tsuen River and tributaries (DUDGEON & LAM 1985a). The test species were *Brotia hainanensis* and *Melanoides tuberculata* (Thiaridae), *Sinotaia quadrata* (Viviparidae), *Physella acuta* (Physidae), *Radix auricularia plicatula* (Lym-

naeidae), and *Hippeutis cantonensis* and *Biomphalaria straminea* (Planorbidae). They include species typical of the river headwaters (*B. hainanensis*) and of the lower reaches (*H. cantonensis* and *B. straminea*), but were collected from the middle course.

Locomotor patterns of individual snails (using more than 20 replicates of each species) have been followed on water-filled trays in the absence of food (to eliminate any attractant effect), and compared statistically with a null hypothesis of random movement (UNDERWOOD 1977; WEISS 1983). This random-walk model (following UNDERWOOD 1977) proposes that:

- I) snails wander at random on the observation trays and so the angle of orientation is uniformly distributed;
- II) the distance moved by each animal during each observation period is an exponentially random variate.

Possible departures from the model include one, some or all of the following:

- I) there is a preferred direction of movement, so that the distribution of angles of orientation is not random;
- II) the distances moved are not exponentially distributed;
- III) the distances moved by individuals are correlated from one observation period to the next.

Deviations from the null model of random movement may be indicative of optimal foraging movements and, in order to account for these, samples of gut contents of field-collected specimens of each of the test species have been enumerated to indicate dietary preferences (DUDGEON & YIPP 1985).

When compared with a random-walk model, only *B. hainanensis* shows a distinct tendency towards directional movement, with most individuals of the remaining species moving randomly (LAM & DUDGEON 1985a). However, the requirement of the random-walk model for an exponential distribution of distances moved is not fulfilled by any species, reflecting a lack of very small movements by the test snails. If the snails move at all, they cover a distance equivalent to at least one body length. Nevertheless, the distance an individual moves during one observation period is, in general, independent of the distance that it had moved during the previous period, thereby lending support to the random-walk hypothesis. One striking observation is the tendency for *P. acuta* to move almost twice as quickly as *B. hainanensis*, the second fastest snail.

There are departures from the random-walk model with regard to distance covered among all of the test species; otherwise, only the directional walk of *B. hainanensis* and the speed of movement by *P. acuta* are worthy of note. The lack of small displacements in the movements of all species can be understood in relation to feeding behaviour since it will be advantageous for a consumer to travel a minimum distance of one body length, if it is to move at all, thereby avoiding the food patch which has just been grazed. Deposit-feeding marine animals show similar minimum-distance movements (SCHEIBLING 1981).

Directional movement is adaptive for most consumers because areas depleted previously are avoided and foraging range is maximized. Such movement is seen in some marine primary consumers (SCHEIBLING 1981; THOMPSON & THOMPSON 1982) but not others (UNDERWOOD 1977). Directional movement in *B. hainanensis* can be explained dietary terms: this snail feeds on periphyton but also consumes leaf litter and has distinct preferences for particular species (DUDGEON 1982f). As the

preferred foods of *B. hainanensis* will be patchily distributed, it can be expected that movement by this species will deviate from a random-walk model.

Physella acuta has an unusually rapid rate of movement, which may be attributable to a narrow dietary spectrum. The snail feeds primarily on detritus and periphytic algae, especially diatoms, whereas *B. straminea* (for example) ingests algae, detritus, allochthonous litter, tiny invertebrates and fine sand particles, but few diatoms (DUDGEON & YIPP 1985). Since periphyton patches that are rich in diatoms are unpredictably distributed, it is probable that rapid movement by *P. acuta* reflects the requirement for a large foraging range that arises from dietary specialization. By the same token, when the food resource is uniformly distributed, or the consumer has a broad diet, minimal foraging movements (and locomotory costs) are optimal, resulting in maximum net rate of energy intake for microphagous consumers.

A parallel with the patterns of movement of *P. acuta* is apparent in the locomotion of the North American caddisfly *Dicosmoecus gilvipes* (Limnephilidae). Larvae of this species move about randomly on the stream bed although periphyton food is locally limited and patchily distributed (HART & RESH 1980). Prior to pupation, however, when food requirements increase, larvae move much (300%) faster so increasing the chances of encountering rare but preferred food (HART & RESH 1980).

One aspect of optimal foraging movement will involve food-finding strategies; other components concern the behaviour of a primary consumer when the food is located, and the modification of search strategies according to hunger levels. Observations of *P. acuta*, *R. auricularia plicatula* and *B. straminea* have revealed noticeable interspecific differences in these respects (DUDGEON & LAM 1985b). Increased hunger levels alter foraging patterns, and cause *R. auricularia plicatula* and *B. straminea* to move more rapidly, with starved individuals of the former species exhibiting a tendency towards unidirectional movement. The locomotory pattern of *P. acuta* is, by contrast, unaffected by hunger levels. This snail is the fastest-moving species tested and an increase in speed by starved animals may not be feasible if the snails are already 'running as fast as they can'.

In the presence of food, *R. auricularia plicatula* and *B. straminea* slow down and make frequent turns, a movement pattern which tends to prevent them from straying from a food patch (DUDGEON & LAM 1985b). Neither species can detect food from a distance, and this ability seems to be lacking in pulmonate snails (BÖVJERG 1968; TOWNSEND 1973). However, the test species do alter their foraging patterns according to circumstances, and conform more closely to the predictions of optimal foraging theory when starved and facing an immediate need to increase rates of energy acquisition. Apparently, behaviour is adjusted in such a way as to increase net rates of energy intake.

Although most Hong Kong freshwater snails move suboptimally in relation to the predictions of optimal foraging theory (DUDGEON & LAM 1985a), this behaviour may be 'good enough' from the point of view of snail fitness. Moreover, in times of stress some pulmonates can alter their foraging strategies in response to feeding regime and forage 'more optimally' when starved (DUDGEON & LAM 1985b). These snails, and other invertebrates, may be using 'rules of thumb' (TOWNSEND & HUGHES 1981; HAINSWORTH & WOLF 1983), that will approximate the maximum rate of energy return for a consumer in a variable environment, rather than conforming precisely to an optimal model. Such a strategy may be common among invertebrates which may face constraints upon information gathering and

processing (TOWNSEND & HILDREW 1980). Only those snails with highly-patchy food resources (*B. hainanensis*, for example) exhibit foraging patterns matching the predictions of optimal foraging theory, and it is significant that the animals which these predictions fit best – predators, parasitoids and nectarivores (HEINRICH 1983) – exploit resources which are distributed more unpredictably than the food of the majority of primary consumers. A comparison of the results of research on Hong Kong lotic invertebrates provides support for this generalization, with predators conforming more closely than primary consumers to the predictions of optimal foraging theory.

Feeding apparatus and diet: mayfly larvae

Interspecific differences in the diets of Hong Kong stream snails (DUDGEON & YIPP 1985) may be attributable to the morphology of the feeding apparatus. Indeed, the buccal apparatus and alimentary tracts of some freshwater snails are consistent with interspecific dietary differences (KESLER et al. 1986; BLINN et al. 1989) or feeding efficiency (BARNESE et al. 1990). In other snails, however, there is an absence of significant associations between the form of the feeding apparatus (the radula) and trophic or behavioural parameters, which suggests that some variation in radula tooth shape may be nonadaptive (SMITH 1989).

Mouthpart morphology has been linked to diet in some lotic insects (SEPHTON & HYNES 1983), and intraspecific differences in the food habits of early- and late-instar larvae (BROWN 1961; FULLER & STEWART 1977; SEPHTON & HYNES 1983; YULE 1986; LI & GREGORY 1989) may be accompanied by changes in mouthpart size and shape, although ontogenetic changes in foraging behaviour are also important (HART & RESH 1980; LI & GREGORY 1989).

Mayfly larvae show a great diversity of mouthpart form, and provide an opportunity to relate structural adaptations to function in the lotic environment. Such work has been undertaken for nine species from six families of mayflies that are common in Hong Kong streams. The species investigated included five from Tai Po Kau forest Stream and four from Lam Tsuen River. There is considerable inter-family variation in the morphology of the four basic mouthpart components, the labrum, mandibles (paired), maxillae (paired) and labium (a fused pair of second maxillae), but relatively small differences within families. The mouthparts of the heptageniids *Epeorus* (*Iron*) sp. and *Cinygmmina* sp. are concealed beneath the flattened head capsule, and the labrum is expanded so as to cover the mandibles and maxillae when viewed from below. The labial palps bear a distal crown of setae and, like the well-developed maxillary palps (Figs 24, 25), may serve to 'comb' or brush fine particles from stone surfaces into the buccal cavity. The maxillary galea-lacinia (the main body of the maxilla) of these insects also bears bristles, and in *Cinygmmina* sp. the apex is fringed by a row of pectinate spines (Fig. 25). The mandibles are small in comparison with the size of the labium (Figs 24, 25) with slender incisor teeth at the apices. As in other mayflies, the molar areas of the left and right mandibles are differentiated in such a way as to facilitate articulation and efficient grinding of food particles. The prosthecae (between the incisor and molar regions) are represented by a few setae.

Choroterpes (*Euthraulus*) sp. and *Habrophlebiodes gilliesi* (Leptophlebiidae) are similar with respect to mouthpart morphology. Unlike heptageniids, leptophlebiid

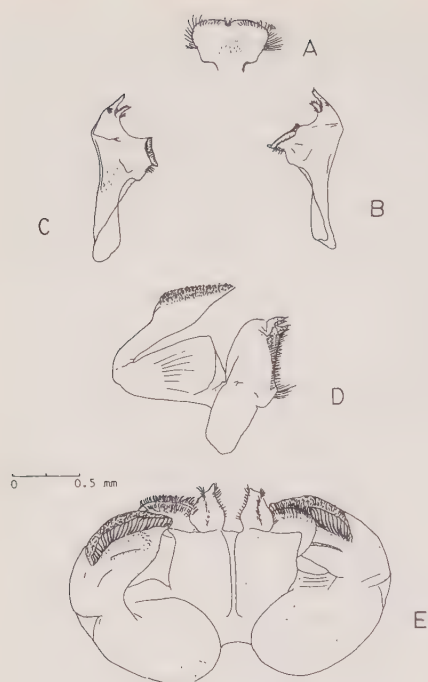


Fig. 24. *Epeorus* (*Iron*) sp. mouthparts (Heptageniidae): A, labrum; B & C, right and left mandibles; D, maxilla; E, labium.

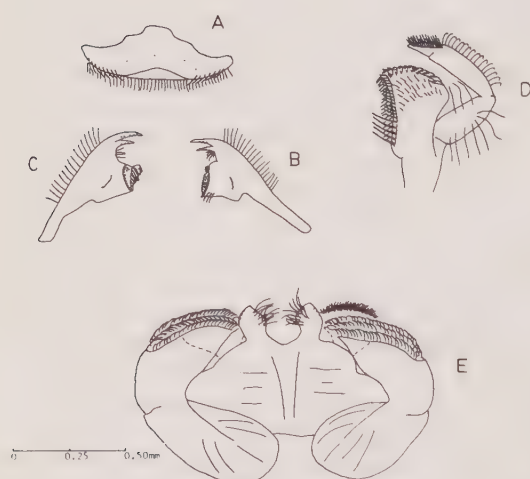


Fig. 25. *Cinygmmina* sp. mouthparts (Heptageniidae): A, labrum; B & C, right and left mandibles; D, maxilla; E, labium.

mouthparts are situated at the front of the head capsule and are not concealed when viewed from above. The leptophlebiid labium is expanded but the palps are more slender and less hirsute than those of heptageniids (Fig. 26). The maxillary palps are likewise less well-developed, but the maxillary galea-lacinia is relatively broad and densely clothed with setae along the inner margin and crown. The mandibles are

stouter and more massive than those of the heptageniids: the paired apical incisors are still rather slender but have forked tips, the prosthecae comprise spines with brush-like apices, while the left molar region is considerably elaborated into a saw-like process (Fig. 26). Like the heptageniids, leptophlebiid mouthparts are modified for gathering fine particles and brushing them into the mouth. However, the relatively stout mandibles suggest that leptophlebiids may also take in larger particles that need to be macerated.

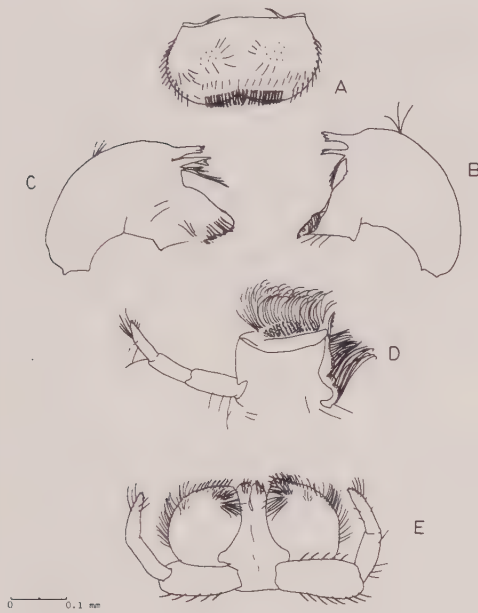


Fig. 26. *Habrophlebiodes gilliesi* mouthparts (Leptophlebiidae): A, labrum; B & C, right and left mandibles; D, maxilla; E, labium.

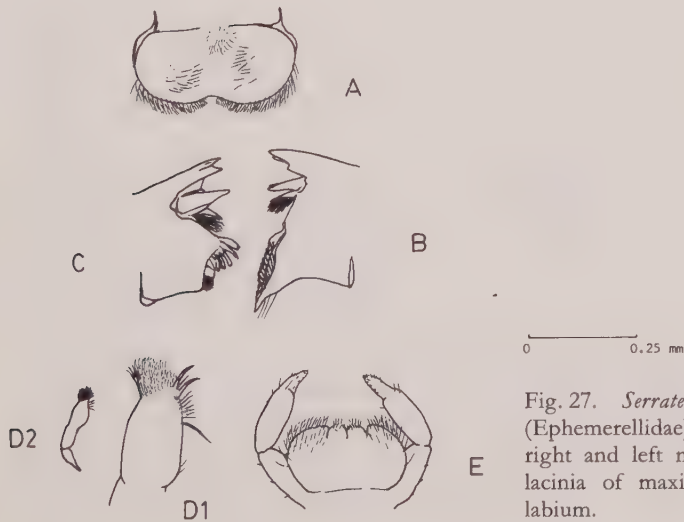


Fig. 27. *Serratella* sp. mouthparts (Ephemerellidae): A, labrum; B & C, right and left mandibles; D1, galealacinia of maxilla; D2, maxilla; E, labium.

The ephemerellid mayfly *Serratella* sp. has a labium similar in general appearance than that of leptophlebiids, but the labial palps are relatively long (Fig. 27). *Serratella* sp. lacks maxillary palps however, and setae are confined mainly to the crown of the maxillae. The mandibles are robust, with incisors, prosthecae and molar region all well developed. The left molar bears sharp-edged processes which may be used to cut up food particles. The structure of these mouthparts suggests some collection of fine particles using the labial setae, but the relatively stout mandibles indicate a primarily macrophagous feeding mode.

The baetid mayflies *Pseudocloeon* (*sensu lato*) sp. and *Platybaetis* sp. have a greatly reduced labium when compared to the preceding families, and the labial palps are stout, bearing spines rather than setae (Fig. 28). The maxillary palp is reduced and naked, while the apex of the maxilla bears teeth and short spines but no setae. The incisor region of the mandible comprises a group of fused, blunt teeth, the prostheca forms a well-developed spine with serrated tip, and there is some differentiation between the left and right molar regions (Fig. 28). The grinding role seems to be confined to the right molar region. The mouthpart structure suggests that these insects feed by picking up food particles (such as diatoms), macerating and swallowing them singly. Baetids lack the strong cutting mandibles of *Serratella* sp. as well as the collecting or brushing bristles and setae of heptageniids and leptophlebiids.

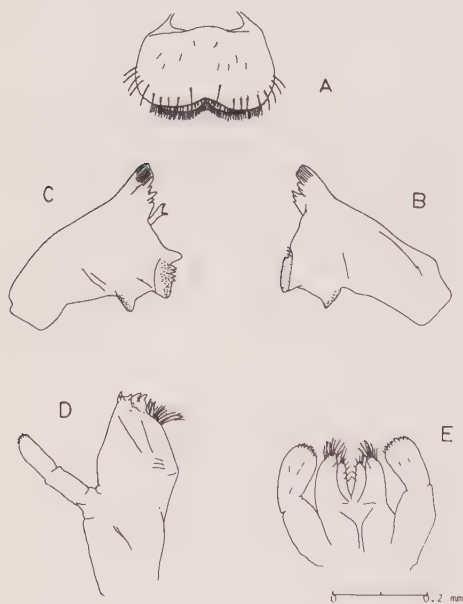


Fig. 28. *Pseudocloeon* sp. mouthparts (Baetidae): A, labrum; B & C, right and left mandibles; D, maxilla; E, labium.

The mouthparts of *Caenodes* sp. (Caenidae) are similar to those of *Serratella* sp., although the caenid differs from all Hong Kong Ephemerellidae in the possession of a long maxillary palp (Fig. 29). The galea-lacinia of the maxilla bears stout spines at the apex but rather few setae. The mandibles resemble those of a leptophlebiid, although the incisor teeth are relatively massive and stout (Fig. 29). There are no

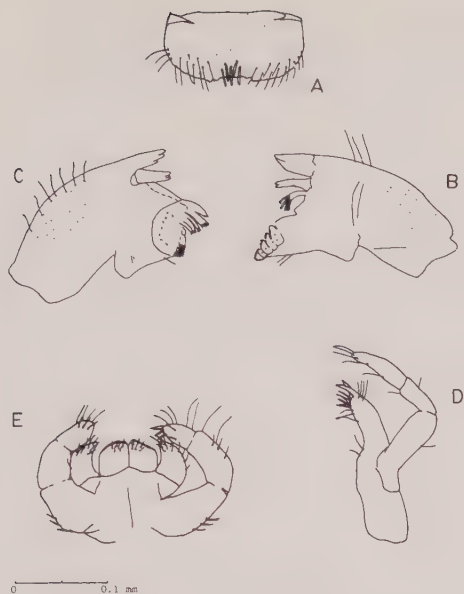


Fig. 29. *Caenodes* sp. mouthparts (Caenidae): A, labrum; B & C, right and left mandibles; D, maxilla; E, labium.

clear indications as to the feeding habits of *Caenodes* sp., but the mouthparts lack setal fringes for the collection of fine particles.

The labium and maxilla of the burrowing mayfly *Ephemera* (*Ephemera*) *spilosa* resemble those of *Caenodes* sp. Nevertheless, the palps associated with both structures are greatly enlarged in the former species, and the maxillary palps are more densely clothed with setae (Fig. 30). The mandibles bear dorsal tusks as an aid to burrowing, and the incisor region is somewhat truncated. The molar area is well-developed with pronounced ridges which appear to have a grinding function (Fig. 30). The general structure of the labrum does not vary greatly among mayfly families (although the shape may differ), but that of *E. (E.) spilosa* is unusual in the possession of serrated spines in the apical notch (Fig. 30).

There is an array of differences in the form of the mouthparts of the six mayfly families considered above. These differences are summarized in Fig. 31 which gives a diagrammatic representation of the arrangement of the mouthparts in each group. Morphology is viewed generally as reflecting an individual's match with the habitat template, and we would expect differences in feeding structures to be manifested in dietary composition. Analysis of the diets of these nine mayfly species does not, however, support this expectation (Fig. 32). Fine particulate detritus (undifferentiated organic matter) dominates the gut contents of all mayflies except *Serratella* sp. The gut contents of this species comprise mostly allochthonous detritus (leaf-litter fragments), which also makes up around 30% of *E. (E.) spilosa* diets. Apart from these two exceptions, however, the mayfly diets appear quite similar.

An interspecific comparison of dietary composition using a standard overlap index (PIANKA & PIANKA 1975; MATTHEWS et al. 1982), where values range from zero (no overlap) to one (complete overlap) and values less than 0.75 indicate a significant difference between species, showed that *Serratella* sp. gut contents were

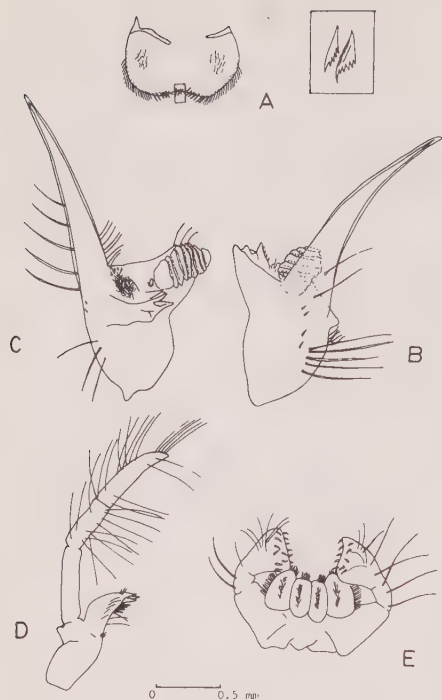


Fig. 30. *Ephemera (Ephemera) spilosa* mouthparts (Ephemeridae): A, labrum; B & C, right and left mandibles; D, maxilla; E, labium.

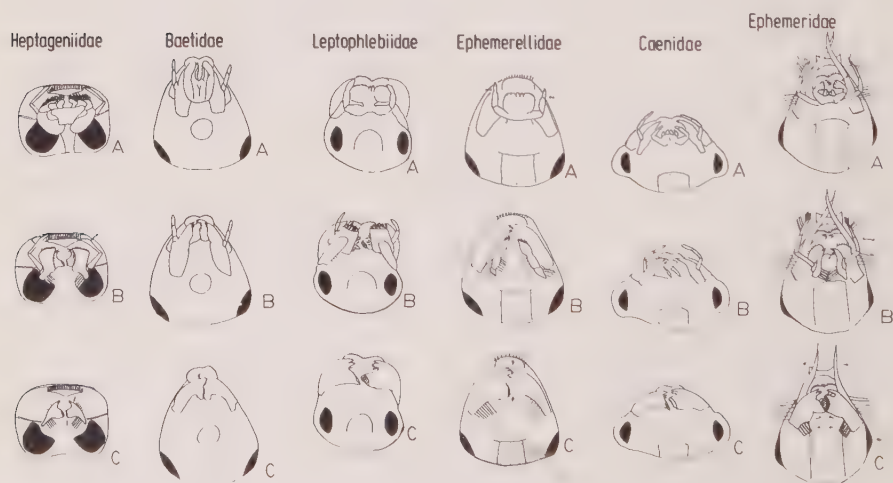


Fig. 31. Diagrammatic representation of mouthpart arrangements in six mayfly (Ephemeroptera) families: A, ventral view of mouthparts; B, ventral view of mouthparts with labium removed; C, ventral view of mouthparts with labium and maxillae removed.

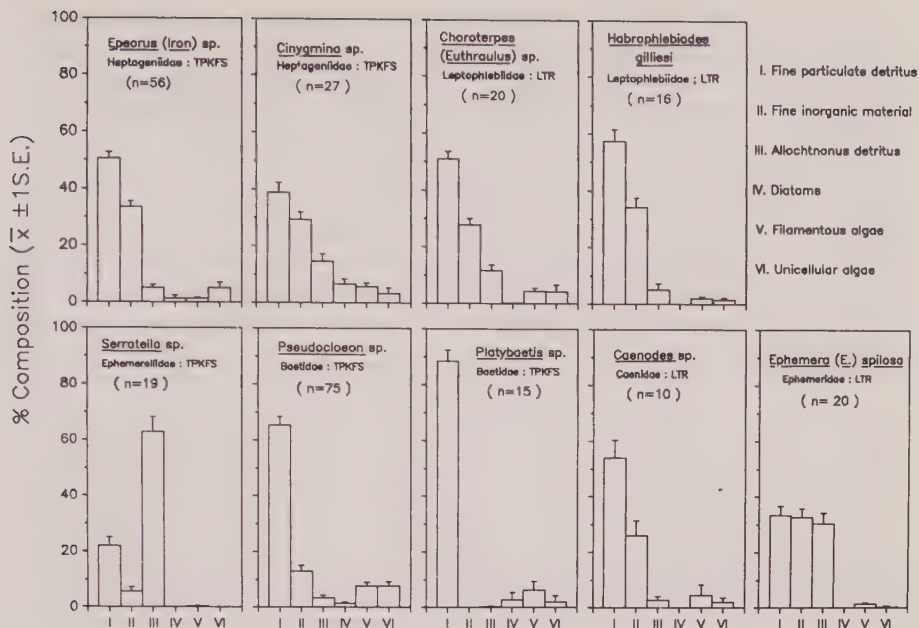


Fig. 32. The composition (mean % \pm 1 S.E.M.) of the gut contents of nine mayfly (Ephemeroptera) species from Tai Po Kau Forest Stream (TPKFS) and Lam Tsuen River (LTR).

Table 9. Dietary overlap among Hong Kong mayfly larvae. Overlap values range from 0 (no overlap) to 1 (complete overlap) (PIANKA & PIANKA 1976); values ≤ 0.75 indicate significant dietary differences.

	E	C	Ch	H	S	P	Pl	C
<i>Epeorus</i> (E)	*							
<i>Cinygmia</i> (C)	0.97	*						
<i>Choroterpes</i> (Ch)	0.98	0.97	*					
<i>Habrophlebiodes</i> (H)	0.99	0.96	0.99	*				
<i>Serratella</i> (S)	0.40	0.56	0.50	0.39	*			
<i>Pseudocloeon</i> (P)	0.92	0.87	0.94	0.93	0.38	*		
<i>Platybaetis</i> (Pl)	0.82	0.76	0.86	0.86	0.33	0.97	*	
<i>Caenodes</i> (C)	0.98	0.93	0.98	0.99	0.39	0.95	0.89	*
<i>Ephemerella</i>	0.86	0.93	0.89	0.85	0.75	0.72	0.60	0.81

different from those of all other species (Table 9). The diet of *E. (E.) spilosa* is notably different from *Serratella* sp. and the two baetids only. On the face of it, these data indicate that – at least within the order Ephemeroptera – there is only a rather weak relationship between mouthpart morphology and the type of food that an animal ingests. It is therefore not surprising that when the analysis was extended to consider intraspecific dietary variation between early and late instars of *Pseudocloeon* sp. and *Epeorus (Iron)* sp., overlap values of 0.99 were recorded within both species.

What sense can we make of the similarity of diets in animals that have differently-formed feeding structures? We might conclude that the mouthparts of mayflies are not at all adaptive, and that the range of morphologies seen in extant mayflies is merely a result of evolutionary serendipity. This seems unlikely because the range of mouthpart forms observed in the Hong Kong mayflies are clearly derived from modification of some basic plan and, if mouthpart morphology is unimportant, it is parsimonious to assume that the unmodified basic plan would be retained. Alternatively, since the amount of resources an animal obtains will have positive effects upon fitness, it is a reasonable assumption that structures for gathering resources are strongly influenced by natural selection. Why, then, are there few differences between the dietary composition of animals with markedly different mouthparts?

One possibility is that despite morphological variation, dissimilar mouthparts may be used to ingest the same foods through the use of different feeding movements, as has been recorded among intertidal snails (HAWKINS *et al.* 1989). Another factor complicating investigations of lotic insect feeding habits is that mouthparts of a particular form may be used in more than one feeding mode (McSHAFFREY & McCAFFERTY 1986, 1988). This may have the result that species with similar feeding apparatus (for example, those within the same family) might use them in different ways (McSHAFFREY & McCAFFERTY 1988). The ability of an animal to use more than one mode of feeding complicates the problem of placing species into functional feeding groups, a difficulty discussed above in relation to the River Continuum Concept. One way out of this dilemma is to erect a new scheme using a more mechanical approach to delineate the functional feeding groups of at least those benthic insects that feed on fine particles (McSHAFFREY & McCAFFERTY 1988), but this approach has yet to be adopted widely.

Considering the Hong Kong data, but leaving aside *Serratella* sp. which is a specialized consumer of allochthonous litter, it may be that the general lack of inter-family differences in diet reflects the microdistribution of these mayflies in streams. Ephemerids burrow into sandy sediments in microsites sheltered from the main force of stream flow; caenids also favour sheltered sites but sprawl on the stream bed or dwell in the interstices of the substratum. Heptageniids are found on and under rocks in fast current where their flattened body form keeps them away from the main force of the current. Baetids have streamlined fish-like bodies and are found on stone surfaces exposed to the full force of the current. The leptophlebiids studied here, by contrast, live beneath stones in moderate to slow currents. Given such differences in microdistribution, it is plausible that mouthpart morphology reflects methods for gathering the same type of food under various microenvironmental conditions. Accordingly, while the dietary similarity of two species in the same family reflects morphological and microhabitat correspondence, dietary similarity between families can be viewed as a consequence of animals attaining the same dietary ends by employing dissimilar feeding devices under disparate conditions. We might say that mayflies using different tools under a variety of circumstances are able to achieve the same ends.

The mayfly example can be used to highlight other points concerning adaption. Firstly, there may be more than one solution to a particular adaptive problem, and instances of each outcome can be found within a single habitat. This point has been highlighted in a recent review by ARENS (1989), who demonstrated that there is a

range of solutions to the single adaptive problem of grazing on the thin epilithic algal layers attached to stones. Secondly, given that there may be multiple solutions to adaptive problems, it is not useful to persist with enquiries as to which adaptation is the better or best one. Finally, as an examination of mayfly mouthparts makes clear, solutions to problems set by the environment do not arise *de novo* out of thin air. Instead, alteration or elaboration of existing structures such as the mandibles, maxillae and labium provide the means by which mayfly feeding devices are adjusted to local conditions. Natural selection modifies existing structures, and must therefore operate within the constraints of available variation among those individuals constituting a population. However, this restriction does not preclude the convergent evolution of similar types of feeding apparatus in unrelated taxa (ARENS, 1989).

Feeding apparatus and diet: net-spinning caddisflies

For most lotic invertebrates, a study of the diet and feeding apparatus involves investigation of gut contents and mouthparts. This approach is insufficient for certain filter-feeding insects (many caddisflies and some chironomids) which spin silken capture nets in order to obtain food. The use of such nets is perhaps the preeminent adaptation to life in running waters, as it depends upon a unidirectional flow of water which is sieved in order to obtain food. Among caddisflies, the Stenopsychidae, Philopotamidae and Hydropsychidae comprise species which depend, for some or all of their lives, on a filter-feeding mode of existence. The Dipseudopsiidae and Polycentropodidae also use nets or silken snares to assist in food acquisition. However, hydropsychids are the predominant filter-feeders in Hong Kong streams, although *Stenopsyche angustata* (Stenopsychidae) and various *Chimarra* species (Philopotamidae) are also common.

Filter-feeding caddisflies the world over exhibit a pattern of apparent segregation of mesh sizes; in other words, capture-net mesh sizes vary within and between species in such a way as to suggest partitioning of food resources to reduce intra- and interspecific competition. Some of these interspecific differences in net dimensions are remarkably consistent across geographic regions: for example, philopotamids spin very fine-meshed nets (between $0.8 \times 3 \mu\text{m}$ and $0.8 \times 9 \mu\text{m}$ among *Chimarra* species; WALLACE & MALAS 1976, see also CARTWRIGHT 1990), and macronematine hydropsychids (*Macrostemum* and *Macronema* spp.) construct nets which have the smallest pores among all the Hydropsychidae (WALLACE & MERRITT 1980). Such consistency within genera suggests a phylogenetic constraint on mesh size, implying that capture-net structure is unlikely to be the direct result of competition between members of the caddisfly assemblage within a particular stream or drainage basin. Among the subfamily Hydropsychinae, however, there is greater flexibility in mesh size, and interspecific differences – as well as variations between instars of the same species – have been recorded (WALLACE 1975a, b; MALAS & WALLACE 1977; WALLACE et al. 1977; WALLACE & MERRITT 1980; BOON 1984).

There has been considerable debate as to whether mesh-size differences reflect competition or other processes (WALLACE 1975a; MALAS & WALLACE 1977; WALLACE et al. 1977; ALSTAD 1982, 1986; THORP 1983, 1984; MILLER 1984; TANIDA 1984; THORP et al. 1986). The balance of opinion seems to have shifted away

from competition as a causative factor (ALSTAD 1987), although the matter is not yet settled. Regardless of the reason for differing mesh sizes, however, we might expect that net design (which can be regarded as equivalent to the 'feeding apparatus' of hydropsychids) would influence the diet of the net builder. Relating food eaten to mesh dimensions thus gives us a way of investigating how an individual's interactions in the stream habitat are influenced by behavioural and morphological adaptations.

Hong Kong has a rich hydropsychid fauna, but a single stream will support only a subset – numbering about eight – of the local species. Investigations in Tai Po Kau Forest Stream and the Ho Chung River have involved attempts to relate capture-net

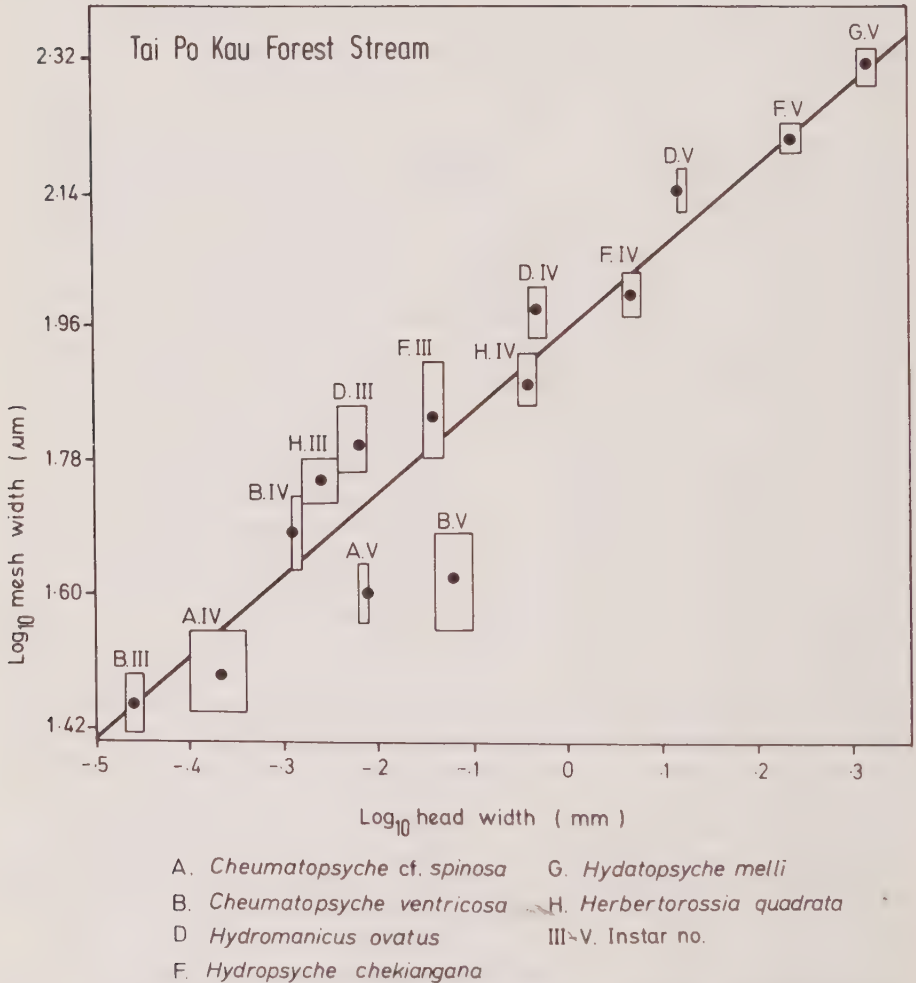


Fig. 33. The relationship between larval head width and capture-net mesh size among hydropsychid caddisflies (Trichoptera) in Tai Po Kau Forest Stream. Best-fitting line calculated by the method of least mean squares.

mesh sizes to caddisfly diets. One obvious point emerging from this research is the dependence of mesh dimensions on caddisfly size; specifically, the width of the head capsule. There is a clear relationship between these parameters in both streams (Figs 33 & 34) with the consequence that mesh size increases as an individual passes through successive larval instars. In addition, bigger species of Hydropsychinae spin more coarse-meshed nets than smaller ones.

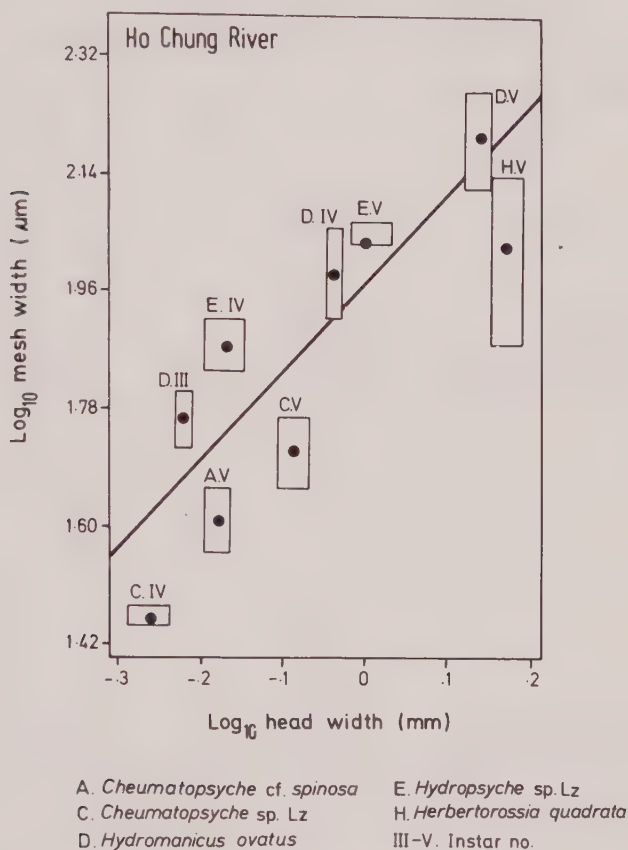
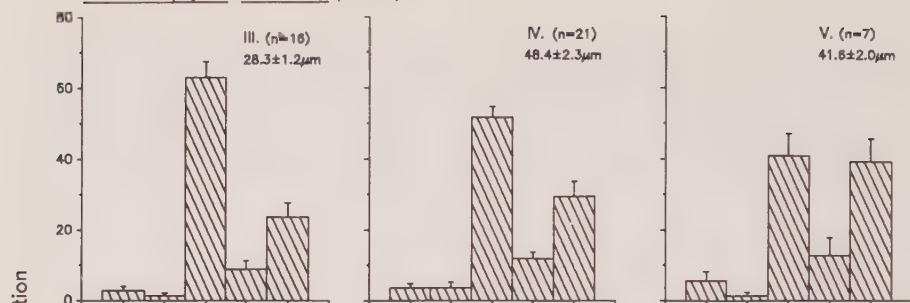
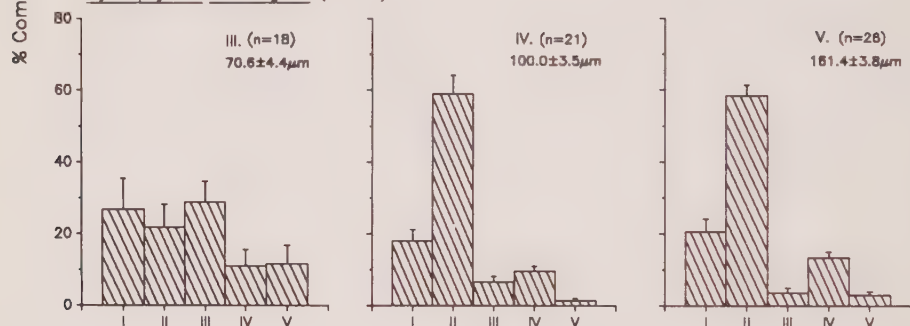
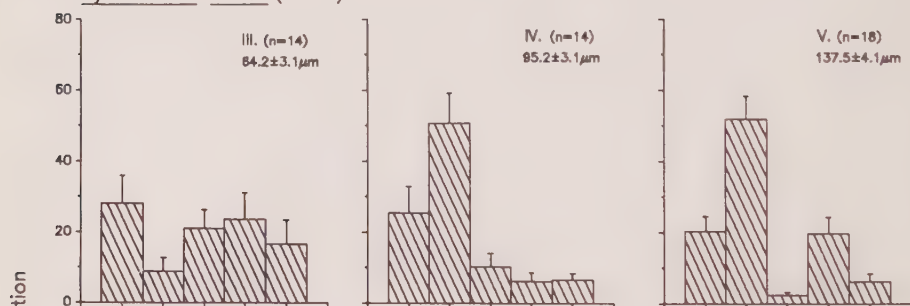
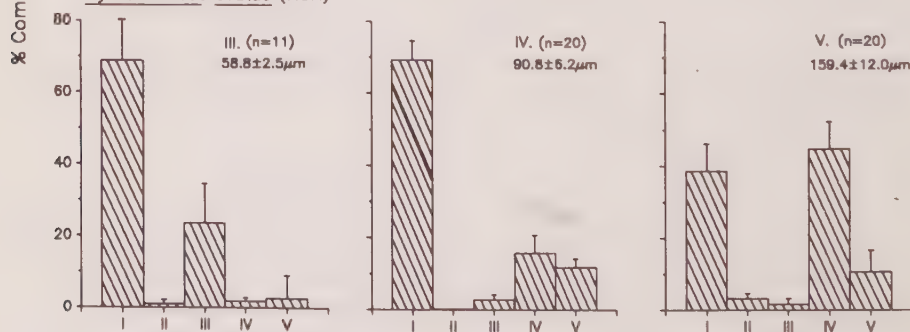


Fig. 34. The relationship between larval head width and capture-net mesh size among hydropsychid caddisflies (Trichoptera) in the Ho Chung River. Best-fitting line calculated by the method of least mean squares.

How do these differences in mesh size relate to diet? Animals spinning fine-meshed nets seem to consume more fine detritus (derived from allochthonous litter breakdown) and fine particulate organic material (FPOM, with no definable structure); those with coarser meshes consume more algae and drifting animals, as well as greater amounts of leaf-litter fragments (Figs 35 & 36). In general then, fine-meshed capture nets lead to a diet comprising fine detritus of various origins

Cheumatopsyche ventricosa (TPKFS)Hydropsyche chekiangana (TPKFS)Hydromanicus ovatus (TPKFS)Hydromanicus ovatus (HCR)

I - Animals II - Filamentous algae III - Fine detritus
IV - Litter fragments V - FPOM

while coarser nets promote the ingestion of animals and algae, with leaf litter as a significant, but less important, dietary component. This generalization appears to apply in Tai Po Kau Forest Stream and Ho Chung River, and also holds true for comparisons between instars of the same species (Fig. 35). *Herbertorossia quadrata* is one exception to the tendency of species spinning coarser nets to ingest more algae and animals (Fig. 36), and there is a clear difference between the diet of this species and that of sympatric *Hydropsyche chekiangana* which spins a net of almost the same mesh size. This interspecific variation in diet reflects microhabitat preferences: *H. chekiangana* lives on the upper surface of stones while *H. quadrata* lives underneath them. Only the three *Cheumatopsyche* species share this anachoretic habit, and it is notable that these animals and *H. quadrata* have similar diets. The sole discrepancy is the inclusion of more litter fragments in the food of *H. quadrata*, reflecting its coarser net.

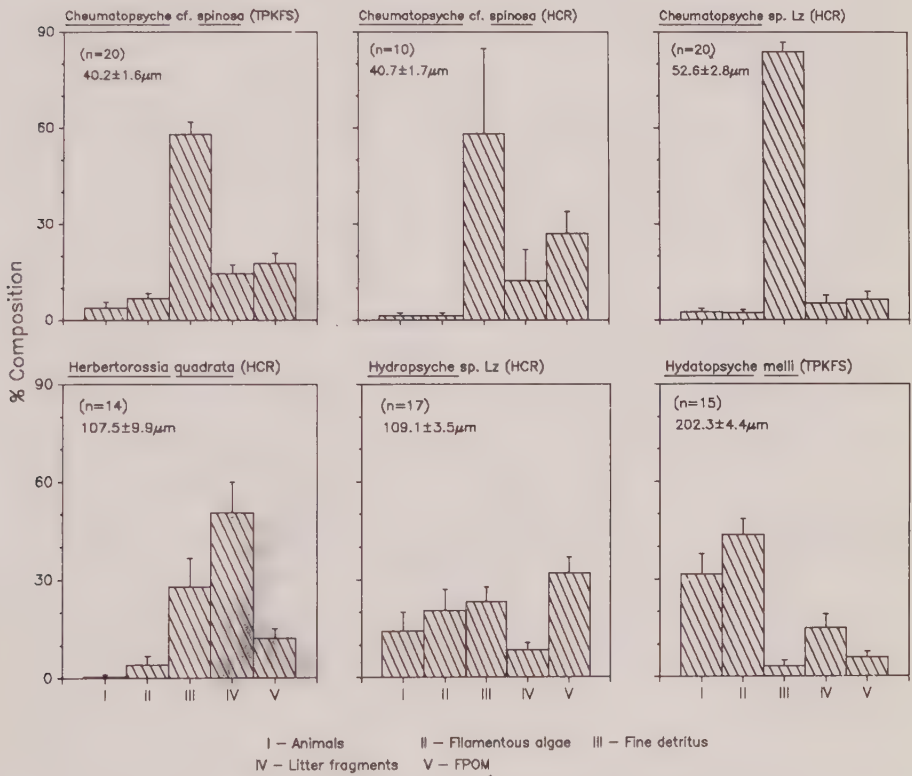


Fig. 36. Interspecific differences in the diets of final-instar hydropsychid (Trichoptera) larvae from Tai Po Kau Forest Stream (TPKFS) and the Ho Chung River (HCR) can be related to capture-net mesh size (μm).

◀ Fig. 35. Intraspecific variations in dietary composition are linked to developmental stage (instars III–V) and capture-net mesh size (μm) among hydropsychid (Trichoptera) larvae from Tai Po Kau Forest Stream (TPKFS) and the Ho Chung River (HCR).

Superimposing the relative dimensions of the capture nets of final-instar larvae in Tai Po Kau Forest Stream (Fig. 37) and the Ho Chung River (Fig. 38), mesh-size segregation is apparent among some species but not others (such as *Cheumatopsyche* spp.). Net dimensions are, however, related to microhabitat occupancy because the mesh size of a functional net is inversely proportional to water flow (GEORGIAN & WALLACE 1981). Accordingly, a caddisfly living in swift current must have a coarse-meshed net if it is to sieve the passing water. Indeed it is striking that *Hydatopsyche melli*, which spins nets with the largest mesh size, lives atop boulders in turbulent 'white-water' sites. Under such circumstances, the diet will include larger particles carried by the fast current, such as drifting animals and strands of filamentous algae as well as some detritus. A coarse-meshed net will filter considerable volumes of water and give the caddisfly a good chance of encountering scarce but easily-assimilated food items such as algae and animals. Less-valuable litter fragments are ingested at times, but can be rejected by the larva pushing them from the net. A significant proportion of the trophic basis of production for larvae spinning coarse-meshed nets is therefore likely to be animal food (*cf.* BENKE & WALLACE 1980).

Caddisflies living beneath stones sieve gently flowing water which transports only small particles. Accordingly, they spin fine-meshed nets which collect detritus and amorphous organic material. The small size of many of the food particles ingested results in a large surface area for colonization by microbes and these, rather than the relatively refractory detritus, may be a major source of energy for the caddisflies.

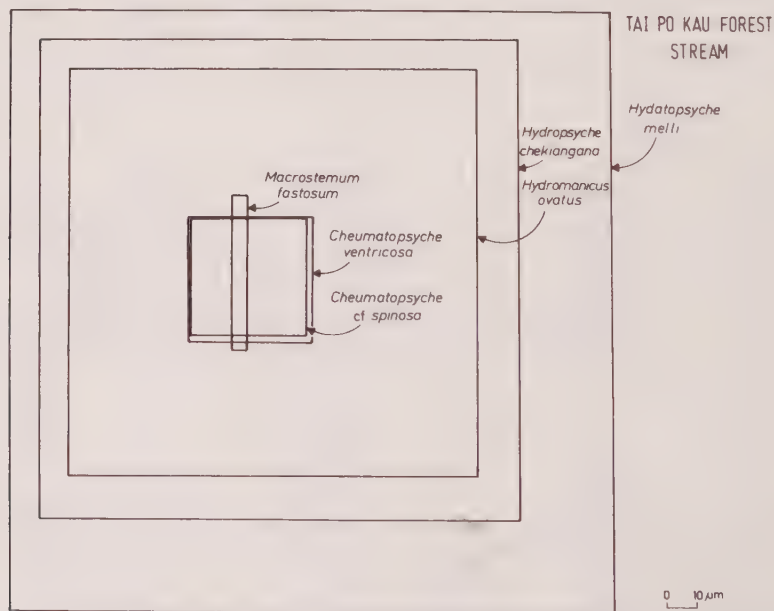


Fig. 37. Relative mesh dimensions of the capture nets spun by final-instar hydropsychid (Trichoptera) larvae in Tai Po Kau Forest Stream.

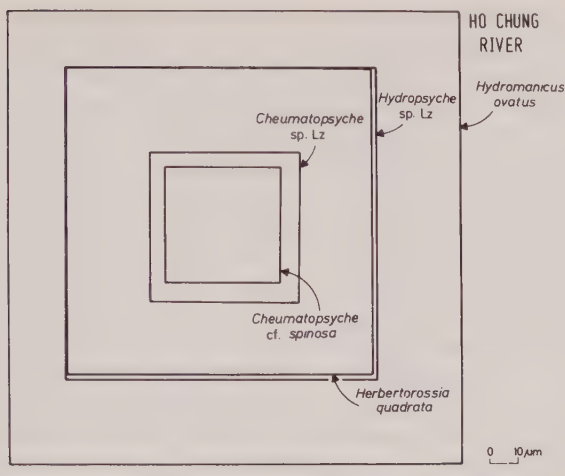


Fig. 38. Relative mesh dimensions of the capture nets spun by final-instar hydropsychid (Trichoptera) larvae in the Ho Chung River.

Substrate composition and current velocity determine the availability of suitable microhabitats in which the capture net of a given species of hydropsychid can be used (MALAS & WALLACE 1977). Current velocity affects the type of suspended food available as well as the efficiency with which a particular net will operate so that net design, microhabitat occupation and diet have become inseparable aspects of caddisfly ecology. Here we can see that caddisfly nets have adjusted through evolutionary time to function effectively under the food regime characteristic of a particular microhabitat. Different mesh sizes result from the action of natural selection producing individuals that maximize net energy intake under disparate conditions and rates of resource supply.

Caddisflies eat different foods as a result of divergence in capture-net design, because the food-capturing mechanism has evolved in response to variation in the types of suspended food available in different microhabitats. Mayflies ingest periphyton and detritus which blankets stream bottom sediments; here, dissimilarity in mouthpart morphology reflects diverse methods of exploiting the same type of food in different microhabitats. In consequence, mayflies have similar diets despite a divergence of feeding apparatus.

Morphological adaptations for life in running water

Running waters the world over present a similar habitat template for colonizing animals, and the adaptations shown by the stream fauna to physical conditions are therefore alike (HORA 1930; NIELSEN 1950; HYNES 1970). Reference has been made already to life-history differences between fishes (such as Gobiidae) and shrimps (Atyidae and Palaemonidae) inhabiting upstream and lower reaches of rivers (see Part II), and these are associated with divergence of larval morphology. HYNES

(1970) has given an excellent account of the range of adaptations shown by lotic animals which need not be repeated here, while VOGEL (1988; chapters 6 & 7) describes the physics of life in flowing environments. Accordingly, the main categories of adaptation will be summarized only, with brief reference made to examples of aquatic insects in Hong Kong.

Many animals that live on stones are flattened, enabling them to avoid high current speeds by living in the slower current speeds which exist immediately above the substrate. Note that the boundary layer is not a discrete layer of non-moving fluid as is sometimes thought, but rather a "...fuzzy region in which there is a strong velocity gradient" (VOGEL 1988; pg. 110). In Hong Kong streams, water pennies (Coleoptera: Psephenidae) – including the genera *Eubrianax*, *Mataeoapsephus* and *Psephenoides* – provide conspicuous examples of such flattening, but this feature is found in other insect groups. The libellulid dragonfly *Zygonyx iris* has a broad flattened body and splayed legs with well-developed tarsal claws. These morphological features can be related to the usual habit of *Z. iris*, which clings to the upper surface of rocks in fast riffles and cascades just below zones of maximum current velocity (FURTADO 1969; BISHOP 1973; ST QUENTIN 1973; DUDGEON & WAT 1986). Mayflies such as *Epeorus* spp. and *Paegniodes cupulatus* (Heptageniidae), *Platybaetis* sp. (Baetidae), and the ephemereiid *Teloganodes* sp. also exhibit such flattening.

It is a common supposition that the flattened shape of many lotic animals allows them to live within the boundary layer (HYNES 1970; MCSHAFFREY & MCCAFFERTY 1987), although there is also evidence that flattened, substrate-clinging mayfly larvae are better protected from predation (CORKUM & CLIFFORD 1981). The boundary-layer view has, however, been criticised as simplistic (STATZNER & HOLM 1982; STATZNER et al. 1988), although a flattened body can decrease pressure drag on species which live exposed to high current speeds (SMITH & DARTNOLL 1980), especially when combined with appropriate behavioural responses (MCSHAFFREY & MCCAFFERTY 1987). In other cases, a flattened body form is found in thigmotactic species that occupy crevices within cobble sediments, away from exposure to the current (NIELSEN 1950; HYNES 1970; MURVOSH 1971; MCSHAFFREY & MCCAFFERTY 1987). The complexity of the physical environment in streams is highlighted by the range of physical factors operating on an animal atop a stone: diffusion of oxygen through boundary layers, corrosion, lift, friction and drag (STATZNER 1988). The physical significance of these five factors depends on body size, and therefore changes during growth, and is affected largely by the ratio of body length: height as well as alteration of microflow patterns downstream of the animal (STATZNER 1988). A simultaneous effective morphological adaptation to all five factors appears to be physically impossible, and this has the consequence that there is probably no rule of thumb governing the body form of rheophilic animals (STATZNER & HOLM 1982; STATZNER 1988). Extra complications arise because getting down near a surface will provide protection from the forces of fast current, but create the problem that an animal feeding from the water passing by must raise its mouthparts up high enough to encounter adequate flow speeds (VOGEL 1988).

Water pennies provide examples of both rheophilic and anachoretic species, and it is interesting to note that both habits are associated with the flattened body form. The general body shape typical of this group is adjusted – seemingly by varying length:width ratios – to permit exploitation of diverse microhabitats (MCSHAFFREY & MCCAFFERTY 1987). Heptageniid mayflies also include genera which inhabit the

upper (*Epeorus* and *Paegniodes*) and under (*Afronurus*, *Cinygmmina* and *Electrogena*) surfaces of stones, and flattening in stoneflies (Perlidae: Neoperlinae) and the damselfly *Euphaea decorata* (Euphaeidae) seems to be associated with living underneath rather than on top of stones. Flattening must therefore be seen as having evolved in stream insects for a variety of reasons.

Streamlining to reduce drag is a less common adaptation among lotic insects, but those animals displaying it – the baetid mayflies – are abundant in most streams. Other mayflies such as the oligoneuriid *Isonychia kiangsinensis* and the leptophlebiid *Isca purpurea* show streamlining, the body of the latter being rather rounded in cross-section and more fish-like or fusiform than other Hong Kong Leptophlebiidae which are dorso-ventrally compressed. The streamlined mayfly body works in combination with the pilose terminal abdominal filaments or tails. When the larvae raise themselves on their legs with the abdomen hanging free in the water, the tails swing from side to side in the small eddies and keep the body facing directly into the current (HYNES 1970). This directional placement is especially important for *I. kiangsinensis* as it employs a double row of long bristles, which fringe the inner margins of the fore femora and tibiae, to filter food particles from the current (WALLACE & O'HOP 1979).

In fast currents, the typical *Baetis*-type mayfly is accompanied by *Baetiella* and *Pseudocloeon* (*sensu lato*) which have the streamlined body supplemented by a degree of flattening. It is curious that the latter two genera have the middle of the three tails reduced greatly or absent, and Baetidae with progressively-shorter terminal filaments seem to live in habitats with increasing current velocities (DODDS & HISAW 1924; HORA 1930). This observation has been related to the occupation of higher-altitude streams by two-tailed compared to three-tailed baetid larvae (WARD & BERNER 1980; CORKUM & CLIFFORD 1981), but such altitudinal zonation is not apparent in Hong Kong streams. Loss or shortening of the median filament may nevertheless be interpreted as a reduction in the resistance to water flow presented by projecting structures, but the argument is weakened by the observation that some highly-flattened inhabitants of the boundary layer (*Epeorus* spp.) have lost the median filament, while others (*Paegniodes cupulatus*) have not. Nonetheless, it is notable that animals which dwell beneath stones, such as megalopterans (Corydalidae: *Corydalus* and *Neochauliodes* spp.) and whirlygig beetle larvae (*Orectochilus* and *Dineutus* spp.: Gyrinidae), tend to have non-locomotory lateral projections, while those atop stones do not.

True hydraulic suckers which exert negative pressure are rare among stream insects and seem to have evolved only in the Blepharoceridae (Diptera: Nematocera). These insects are confined to torrential streams where they hold on to smooth boulders using four abdominal suckers. Instead of suckers, the ventral surface or body margins of certain stream insects are modified so as to make close contact with the rocky substratum. This increases frictional resistance and, along with appropriate behaviour, will combat lifting forces imposed by the current. The spines fringing the carapace margins of psephenids may function in this way. In *Epeorus* (*Iron*) sp. (Heptageniidae), the first pair of gills are enlarged and turned forwards to meet under the thorax along the ventral mid-line. This increases the area of marginal contact, producing a shallow cup-like structure, and reduces the chances of water flowing under the larva. Mayflies with such structures are more difficult to remove from rocks than those with unmodified gill lamellae (MC SHAFF-

REY & McCAFFERTY 1987), but it is curious that some species inhabiting swift currents have first gill lamellae which are enlarged only slightly (as in *Epeorus* (*Epeorus*) sp.) or lacking entirely (as in *Paegniodes cupulatus*).

Hooks are an alternative attachment mechanism for animals lacking suckers, and claws occur on the abdominal prolegs of caddisfly, corydalid and some beetle (Gyrinidae) larvae. These are enlarged and ornamented (with lateral teeth) to improve purchase in highly rheophilic species such as the caddisfly genera *Rhyacophila* and *Himalopsyche* (Rhyacophilidae). Moreover, BERNER & PESCADOR (1988) report a correlation between tarsal claw size and habitat of mayfly larvae, and it is notable that *Cloeon* larvae which live in standing or slow-flowing waters have rather long, thin tarsal claws when compared to the short, thicker, toothed claws of baetids (*Baetiella*, *Pseudocloeon*) living in swift currents. In addition, baetids with a reduced terminal filament have subapical setae associated with the tarsal claws which may serve as mechanoreceptors to detect changes in water flow and thus assist in orientating larvae to the current (BERNER & PESCADOR 1988).

Certain psychodid (Diptera) larvae (*Neotelmatoscopus*) employ a combination of small spines and circlets of tiny hooks to maintain a hold on rocky substrata, and these are combined with a flattened body. Simuliids (Diptera) use their salivary glands to spin a small silken mat on the rock to which larvae attach themselves by a circlelet of hooks at the end of the body. Additional purchase in strong currents can be obtained by anchoring hooks on the tip of the thoracic proleg to the silk pad. Aquatic caterpillars (Lepidoptera: Pyralidae: Nymphulinae) live beneath silken sheets which they spin on the upper surfaces of flat rocks. Here they feed, grow and pupate, shielded from the force of the current and protected, to some degree, from predators.

Silk forms the basis of constructional activities by caddisflies, and is used to produce portable cases of sand, small stones, leaf and twig fragments. Inorganic cases are thought to function as ballast (as in *Algaepatus* sp.: Glossosomatidae) but the case of *Psilotreta kwantungensis* (Odontoceridae) is constructed with interior braces of silk and tiny rock fragments to prevent crushing by shifting rocks and gravel during spates (WIGGINS 1977). Hydropsychid larvae build fixed houses that are associated with a capture net for filter feeding, while silk-lined tubes of fine sand are built by xiphocentronids and psychomyiids. Chironomids make fixed tubes also which provide protection during grazing or filter-feeding activities. Details of the adaptive significance of such constructions are given by DUDGEON (1990d), who discusses their role in defense and gaseous exchange.

A major problem associated with living in streams is centred upon the insect respiratory system. In most insects, respiration is accomplished by way of a network of air-filled tubes or trachea through which gaseous oxygen is distributed to various parts of the body. The trachea bifurcate and narrow at the tips to form tracheoles which penetrate the organs and tissues, so supplying oxygen directly. The tracheal system of terrestrial insects originates at a series spiracles along the thorax and abdomen. To permit survival under water, the external respiratory system has been variously modified. Minor adjustment is required in certain beetles and bugs which come to the surface at intervals to renew the supply of air in the trachea. An extension of this pattern involving the use of air tubes to obtain atmospheric oxygen, has evolved independently in the Hemiptera and Diptera but tends to restrict insect activity to near the water surface. Bubble-like air stores under the

wings or beneath short, densely-packed, hydrophobe hairs on the bodies of beetles and bugs keeps the spiracles in contact with air. Oxygen will diffuse into the bubble to replace that consumed by the insect, but only so long as the nitrogen in the bubble has not dissipated. Unfortunately, carbon dioxide produced by insect respiration is highly soluble and quickly passes into the water so that the bubble constituting the air store contracts. The partial pressure of nitrogen in the bubble therefore increases, so the nitrogen diffuses out. Ideally, the process can continue until all the nitrogen is lost but in fact the bubble is renewed at the surface once it dwindles below a critical size (THORPE 1950; HINTON 1976). Nevertheless, provided that dissolved oxygen is freely available, these physical gills or (where hydrophobe hairs are involved) plastrons permit the insect to remain below the surface for hours or even days. Outgrowths of the thoracic spiracles, the spiracular gills of certain Diptera, function in the same way with oxygen obtained from the water via a spiracle-associated plastron.

Aeropneustic insects, such as those described above, have at least one pair of functional spiracles with which they breathe atmospheric oxygen (although this may be from a bubble). Hydropneustic insects, including most amphibiotic insect larvae, use dissolved oxygen obtained by way of cutaneous respiration through the body surface. They are not reliant upon functional spiracles and are independent of aerial respiration. Most of these species require well-aerated water, although certain chironomids survive periods of oxygen depletion through the use of haemoglobin which increases their affinity for oxygen.

Many hydropneustic insects have thin-walled projections from the body containing tracheae. Others bear filamentous bunches or tufts which appear to be outgrowths of the tracheal system. These are termed gills (in Ephemeroptera, Plecoptera, Trichoptera, Lepidoptera and some Coleoptera), filaments (in Megaloptera) or lamellae (in damselflies). The ability to ventilate the gills varies in different groups: some mayflies beat their gill lamellae rhythmically so causing water to flow over the body surface; other mayflies have immovable gills. Where the gills of mayflies do move, the production of water currents over the abdomen may enhance respiration through the body surface as well as through the gill lamellae themselves, although the gills account for the majority of oxygen uptake (ERIKSEN & MOEUR 1990); maximum diffusion gradients are maintained in the face of rising temperature and decreasing dissolved oxygen by increasing gill-beating frequency and the proportion of time spent beating (ERIKSEN & MOEUR 1990). Many caddisflies undulate their abdomen causing a current of water to flow over the gills, while Plecoptera will jerk the body up and down (as if doing 'push ups') when suffering respiratory stress. Note that the inability of many hydropneustic insects to ventilate the gills effectively confines them to running water where the unidirectional current ensures a continuous supply of oxygen. HYNES (1970, chapter IX) and RICHARDS & DAVIES (1977, chapter 13) present a more detailed account of respiratory mechanisms, while WILEY & KOHLER (1984) have reviewed the behavioural regulation of gaseous exchange by aquatic insects.

By focusing on morphological adaptations that relate to the problems that insects face maintaining position and respiring in running waters, it has not been possible to give a complete overview of the structural diversity of lotic animals. What should be clear, however, is the range of possible solutions to these adaptive problems, as well as the fact that a variety of morphological outcomes can result from the same

selective pressure (see also ARENS 1989). Thus animals use hooks (and silk), tarsal claws, suckers, or increased marginal contact to maintain a purchase on stone surfaces. Similarly, the evolution of tracheal gills in response to respiratory needs in hydropneustic insects attains different expressions in mayflies, stoneflies, water pennies and Odonata. In contrast to these multiple solutions to the same adaptive problem, a single morphological change – body flattening – can be used as a basis for the exploitation of rock-surface and crevice microhabitats.

Optimal animals revisited

Has natural selection in the stream environment produced individuals with optimal behaviours or morphologies? Investigations of freshwater crabs and predacious bugs indicate that feeding behaviour sometimes matches the predictions of optimality models, and that prey selection involves maximization of benefit/cost ratios. Snail primary consumers show less tendency to behave optimally, although dietary specialists show foraging behaviour which improves their chances of encountering rare but preferred food items. Starved snails also forage more optimally, indicating an ability to modify behaviour appropriately under conditions of food shortage. Nevertheless, animals in streams do not always behave in accordance with our designated best solution; this may be a consequence of responses guided by simple approximations or 'rules of thumb', or could result from prevailing or evolutionary constraints. Current constraints might relate to trade-offs between foraging behaviour and the need to avoid predators, and it is important to note that net rate of energy intake is correlated with, but is not a direct indicator nor the sole determinant of, fitness. Energy maxima obtainable under the combined constraints of predation and (say) time may be far from predicted values and, furthermore, an animal may forage suboptimally while gathering information simultaneously on food, mates, and changing habitat characteristics; together these contribute towards a more optimal life, the suboptimal parts conferring a better whole (HEINRICH 1983; HOWELL 1983).

While there are difficulties in determining what currencies animals use in the decision-making process (and hence what natural selection is maximizing), and although aspects of an individual's behaviour may be suboptimal, there is good reason to suppose that animals will tend towards greater energetic economy (DUDGHEON 1987e). That we cannot show that every animal behaves optimally and conforms to our expectations (PIERCE & OLLASON 1987) does not negate the usefulness of optimality theory, but instead helps us to understand the boundary conditions under which animals operate; i.e. the habitat constraints and lineage-specific biological or evolutionary constraints (STEARNS & SCHMID-HEMPPEL 1987).

The adaptations shown by stream insects must be considered within a framework of historical constraints, since we cannot assume that sufficient genetic variation is present to produce a perfect solution to a particular problem. Accordingly the type of adaptation an animal exhibits will depend upon its ancestry: for example, caddisflies and not mayflies have become the dominant filter-feeders in streams because silk was used during pupal construction by primitive caddisflies, and thence was co-opted into net-building behaviour. Likewise, body-flattening was evolved by mayflies rather than caddisflies because the former group lacked the anal claws

which primitive Trichoptera used to maintain position in strong currents. The flattening has, however, allowed mayflies to exploit both stone surfaces and crevices, while caddisflies have had less success adopting the anachoretic habit.

Although morphologies are not always optimal, it is clear that they are to some extent adaptive, and the relationship between caddisfly diets, capture-net mesh dimensions, and microhabitat occupancy attests to this. Mayfly mouthparts indicate that physical differences in microhabitat will influence efficient food-gathering and hence affect the morphology of the feeding apparatus. Modification of the ancestral plan has therefore taken place in response to the problems of feeding on periphyton and fine detritus in a variety of circumstances. Here the adaptive solution depends on the interaction of microhabitat and phylogeny as represented by the initial form of the mouthparts. Similarly, phylogeny and genetic variability will have influenced the positioning of tracheal gills on aquatic insects; whether gills are on the thorax (stoneflies) or abdomen (mayflies, damselflies and water pennies) is a function of historical accident or contingency rather than representing an optimal solution.

Some of the adaptations of form and behaviour shown by lotic fauna in Hong Kong appear to be optimal, while others are influenced by a variety of constraints. The constrained characteristics may combine to produce a better whole, but whether a feature of form or behaviour is adaptive (enhances fitness) or optimal (maximizes fitness) makes no practical difference to our attempts to understand how individual stream animals interact with their environment, and the way in which those interactions scale up to produce population- and community-level patterns.

IV The human factor

Stream vulnerability

As part of higher landscape units, running waters are particularly vulnerable to disturbance or damage by man. Perturbations within the drainage basin will affect in-stream communities through wash-off or run-off processes and, because of the downhill flow of water, changes in headstream areas alter downstream reaches. Man's modification of stream valleys can also affect the lotic fauna by influencing the terrestrial adult stages of amphibiotic aquatic insects. Indiscriminate use of insecticides, or clearance of riparian vegetation leading to destruction of mating and resting sites, will reduce breeding success and recruitment. The effects of riparian vegetation on in-stream food resources and community structure has been described in Part I.

Channelization, damming and water transfers alter natural stream-flow patterns and discharge regimes, with concomitant effects on seston transport, sediment movements and river-bed characteristics. Dams also impede the breeding migrations of certain decapod crustaceans (mitten crabs, for example) and fishes. Finally, the introduction of exotic plants and animals has disrupted the integrity of Hong Kong's natural stream communities, and this effect has been exacerbated by the tendency for invasions of alien species to be more successful in perturbed or polluted environments.

Pollution

The effects of landscape alteration and pollution on Hong Kong's streams are manifest, and some of the effects of organic enrichment of the Lam Tsuen River by agricultural and domestic wastes have been discussed in Part I. The subject will not be treated at any length here because several excellent reviews of stream pollution are available (e.g. HYNES 1960; HART & FULLER 1976; PASCOE & EDWARDS 1984; WIEDERHOLM 1984; ROUSH et al. 1985; MUIRHEAD-THOMPSON 1987), and there is every reason to suppose that the impacts of pollution upon Hong Kong streams parallel those recorded elsewhere. Moreover, the cures for pollution-related ills are not generally within the purview of the biologist. Once the problem has been identified, solutions lie with governments and those who are in a position to establish legislation relating to waste disposal, land use and so on.

The problem of stream pollution in Hong Kong has been recognized for at least 20 years. During a 1972 stream survey (BINNIE & PARTNERS 1974), 40% of Hong Kong rivers were classified as badly or very badly polluted. In a more recent government survey, 21 rivers and tributaries and almost 200 sites were investigated

during the summer of 1981 (HOLMES 1983). High ammonia and organic nitrogen levels indicated widespread faecal contamination. The overall median value for dissolved oxygen was 4.8 mg/l (approximately half saturation levels), with a minimum of effectively zero, and the median biological oxygen demand (BOD) was 34 mg/l. The last figure compares with 14 mg/l for effluent from a well-run sewage plant. Conditions had deteriorated since the earlier survey: 67% of streams fell into the 'bad' or 'very bad' categories, with only 33% showing 'medium' water quality or better; of these, only 1–8% were classified as 'excellent' (HOLMES 1983).

Clearly, there is reason for concern over Hong Kong's streams, but it must be emphasized that water-quality surveys have tended to concentrate upon lowland sites where human habitation and agriculture are centred. Many hillstreams, by contrast, remain pristine. Recent government legislation affecting livestock farming and waste management, as well as actions that have been taken against some of the most flagrant polluters in the industrial sector (principally dyeing works), allow for some cautious optimism. Nevertheless, the prospect of clean, clear lowland streams remains distant.

River regulation

River regulation, defined in the broadest sense to include the construction of dams and weirs as well as canalization and water transfers, has a long history in Hong Kong. The first reservoir was constructed in 1863 at Pokfulam, little more than 20 years after the colony was established. The dam forming this stream-fed reservoir was so poorly built that it was replaced in 1871 by a larger structure (FESSLER 1974), and the construction of reservoirs continued throughout the succeeding century until the completion of the High Island Reservoir in 1979. The latter is peculiar in that, like Plover Cove Reservoir, it was formed by dredging, damming and draining a marine inlet. Hong Kong's 18 reservoirs have a combined capacity of 586 million m³, and the territory depends upon this storage for the maintenance of a regular water supply.

In recent years the demand for freshwater in Hong Kong has been rising at 11% per year. Increasing demand from a growing population, and periodic droughts in years with lower-than-average rainfall, have forced Hong Kong to import water purchased from China. The volume received has risen from an annual figure of 68 million m³ in 1964 to a projected volume of 620 million m³ in 1995. This water is pumped from the East River (a tributary of the Pearl River) and Shih Ma River, via a series of dams, to the Sham Chun Reservoir from where it is piped to Hong Kong. One early purchase of Chinese water in 1963 was carried to Hong Kong by a fleet of tankers (HUNG 1963). Despite these imports, streams remain the main source of water for Hong Kong's reservoirs, because groundwater resources are insignificant (ASTON 1976). Reflecting this fact, 33% of the territory's 1071 km² area has been developed as waterworks catchments.

An unusual feature of Hong Kong's water catchments is the linkage of impounding reservoirs and catchments by a series of underground pipelines and associated pumping stations. By this means water can be transferred from one reservoir to another; for example, water pumped from China into Tai Lam Chung Reservoir can be relocated to Plover Cove or High Island Reservoirs for storage. Of

greater relevance to lotic ecology, however, is the damming of streams and passage of water collected thereby into the pipeline network. Hong Kong reservoirs thus receive stream water from direct catchments including catchwater channels which extend round neighbouring hillsides to bring more inflow (MOLYNEAUX 1977), and also from indirect catchments which may be many kilometres away. At Tai Po Tau on the Lam Tsuen River (Fig. 39), for example, water is collected behind an inflatable neoprene and nylon fabridam from where it can be pumped to Plover Cove Reservoir or the Sha Tin treatment works. This water includes the flow of the Lam Tsuen River, as well as water transferred from Tai Po River, Tai Po Kau Forest Stream, the upper tributaries of the River Indus, and China.

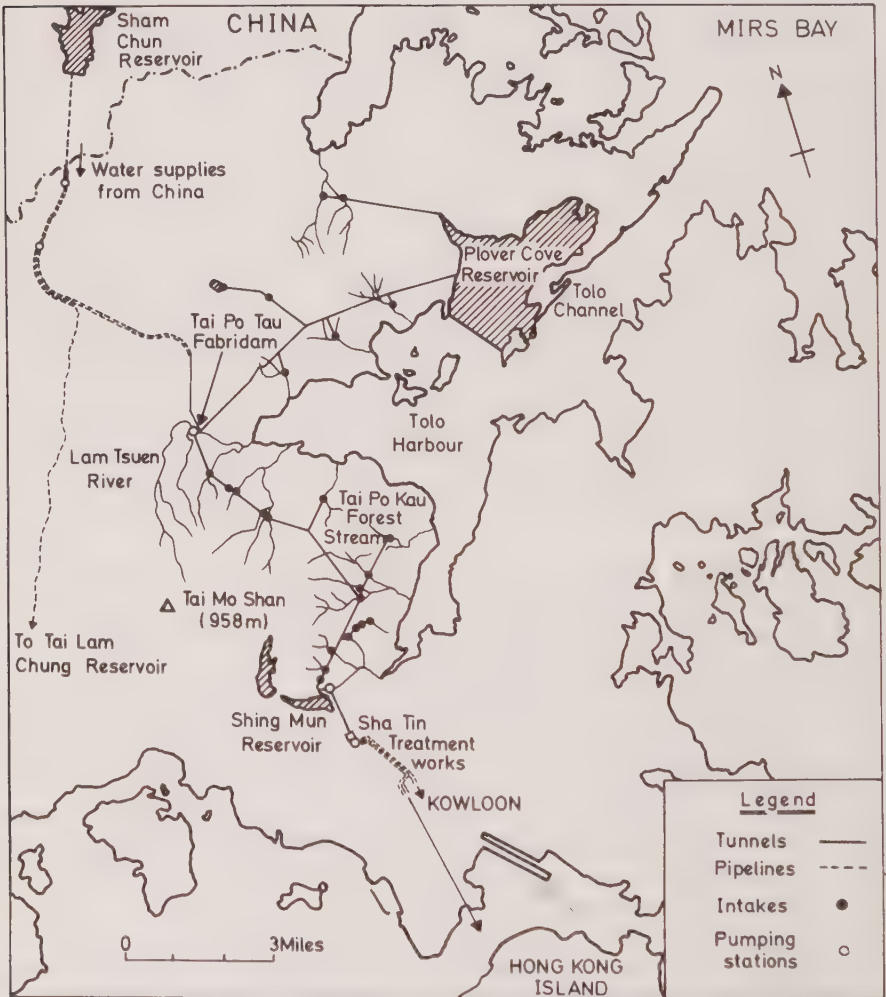


Fig. 39. Part of the network of tunnels and pipelines carrying water from China, as well as from a number of indirect stream catchments, into Plover Cove Reservoir.

Water transfers into reservoirs from indirect catchment streams must have a considerable impact on the ecology of reaches downstream of the site of damming and water capture. Although there is no detailed information on this process in Hong Kong, research on regulated rivers in the temperate zone (e.g. WARD & STANFORD 1979; LILLEHAMMER & SALTVEIT 1984; PETTS 1984; CRAIG & KEMPER 1987) indicate the potential for perturbation of affected reaches downstream. In particular, seston and fine inorganic sediments carried by the stream are diverted and not moved downstream. This affects the food base of the benthic community, as well as the characteristics of the stream sediments. In other words, lowland reaches are changed from the normal situation of sediment deposition and the import of suspended food particles from upstream. Water transfers also reduce absolute discharge volumes downstream, and minimize wet-season flow peaks. Pollution levels are therefore effectively increased, and streams are less likely to be flushed clean by monsoonal rains.

Reduced flow volumes in reaches affected by water transfer are especially marked during the winter dry season. In some cases, the water removed from the stream is almost equivalent to the total discharge, and downstream reaches dry up or the flow disappears into the stream-bed colluvium. Mortality of the stream biota under such circumstances can be high, and although recolonization of the affected area can begin when flow is restored, reestablishment of the original community will depend upon the presence of all of the component species in upstream reaches. Clearly, this presence cannot always be guaranteed.

In some situations, the transfer of water from a stream is so efficient that little of the original flow continues downstream. This is the situation in the lower Lam Tsuen Valley below the Tai Po Tau fabridam, where the river has been reduced to little more than a trickle. The engineer's response to this has been to channelize the old river channel producing a concrete nullah bearing no resemblance to the original lotic habitat. Regulation of the Lam Tsuen River, and accompanying management of the environment, has transformed a slow-flowing lowland river with a rich community of plants and animals into little more than a concrete culvert.

There is a conflict between water-supply demands and stream-management requirements in Hong Kong, and it is inevitable that human needs will prevail over ecological considerations. It is unfortunate, however, that almost every stream of any size in Hong Kong has undergone some degree of regulation, even where this only involves damming to meet local requirements for irrigation water. When combined with the effects of pollution however, human influence on the ecology of lowland rivers in Hong Kong has been ruinous. It remains to be seen whether this devastation can be reversed.

Exotic invaders: overview

Hong Kong serves as the nexus of many trade routes. As such, it is vulnerable to invasion by exotic species transported deliberately or accidentally by importers. The exotic invaders can be divided into three categories: those that were introduced to Hong Kong habitats intentionally (category 1); those which were imported intentionally for a variety of purposes, but escaped and established self-sustaining populations (category 2); and those which were carried to Hong Kong unintentionally.

nally and found their way into streams (category 3). Category 1 species include the poeciliid fishes *Poecilia reticulata* (the guppy) and *Gambusia affinis* (the mosquito fish) which have pan-tropical distributions arising from deliberate introductions as part of mosquito-control programmes. Category 2 comprises species with some economic value, either with regard to aquaculture – as is the case for *Oreochromis mossambicus* (Cichlidae: the tilapia) or as part of the aquarium fish industry (*Xiphophorus variatus* and *X. helleri*: Poeciliidae). The red-eared terrapin (*Pseudemys scripta*: Emydidae), which is imported by pet traders, also seems to have become established in Plover Cove Reservoir. Some Central American cichlid fishes can also be collected from reservoirs on Hong Kong Island, but the populations do not appear to be self-sustaining in the long term.

One animal which has the potential to become a category 2 species is the Japanese freshwater crayfish, *Procambarus clarkii* (Decapoda: Cambridae). This crustacean was introduced into Jiangsu Province in China during the 1930s, and is now cultured from Beijing in the north down to Guangdong Province in the south. The crayfish has also established self-sustaining feral populations in many areas. Although the ecological impact of *P. clarkii* in China is not known, crayfish have important direct and indirect effects on community structure in North American freshwaters (WEBER & LODGE 1990). Since these animals are imported regularly into Hong Kong where they are sold as food or aquarium pets, the potential for escapees to establish themselves must be viewed with concern.

Category 3 species include the Brazilian snail *Biomphalaria straminea* (Planorbidae) which, in its native range, is an intermediate host of the blood fluke *Schistosoma mansoni* that causes bilharzia or schistosomiasis in humans. This snail is thought to have been imported along with ornamental plants by tropical fish traders (YIPP 1990). The apple snail, *Pomacea lineata* (Ampullaridae), also originates from South America, but it is not clear whether this animal was introduced directly into Hong Kong or, first, into the People's Republic of China – where it is used as a food in southern provinces – thence spreading south across the border. The freshwater mussel, *Limnoperna fortunei* (Mytilidae), which was introduced into Hong Kong along with the supply of raw water from China (MORTON 1975), can also be included among category 3 species. A fourth species of mollusc, the snail *Physella acuta* (Physidae), also appears to be an exotic introduction; it is thought to have originated in North America from where – with man's inadvertent assistance – it has colonized freshwater habitats in various parts of the tropics (BROWN 1980).

Hong Kong streams are also host to exotic plants, including the Brazilian water hyacinth (*Eichhornia crassipes*: Pontederiaceae), that is infamous for clogging waterways in the tropics and subtropics (BARRETT 1989), and the floating fern *Salvinia molesta* (Salvinaceae) – also from Brazil – which is a nuisance weed in Southeast Asia, India, Australasia and Africa (ROOM 1990). *Salvinia molesta* was probably introduced into Hong Kong as an aquarium plant. However, like *E. crassipes*, it is widespread in Asia, and establishment in Hong Kong could reflect range extension by exotic Southeast Asian populations. *Eichhornia crassipes* spread may have been enhanced by its use as livestock (especially pig) feed, but *S. molesta* is unpalatable to mammalian herbivores.

Attributes of invasive species

What are the inherent attributes of exotic species in Hong Kong that have made them successful invaders? The answer to this question is that, in some cases, we do not know. For others, however, there are some helpful data. *Biomphalaria straminea*, for example, has been rather well studied. These snails were first noticed in Hong Kong by an amateur malacologist, Mr A. J. Brandt, during late 1973 when they were collected from a small stream in the Lam Tsuen Valley (MEIER-BROOK 1974). Their subsequent colonization of the Lam Tsuen River probably occurred during 1977 (DUDGEON 1983a), and by 1980 the species had become established widely in the lowland areas of the New Territories (DUDGEON & YIPP 1983; YIPP 1990). Although there is evidence of a second more recent (1982) introduction of *B. straminea* into Hong Kong (WOODRUFF et al. 1985), the spread of this snail throughout the New Territories from what appears to have been a single introduction (WOODRUFF et al. 1985) is remarkable. There is also evidence of active dispersal into adjacent areas of the People's Republic of China (LIU et al. 1982), and snails have been intercepted in consignments of aquarium fish imported from Hong Kong into Australia (DUDGEON & YIPP 1983; YIPP 1990). In addition to colonizing the New Territories rapidly, *B. straminea* has prospered in the new environment, becoming especially abundant in slow-flowing streams, irrigation ditches and agricultural channels where densities can exceed 20000 individuals/m² (YIPP 1983, 1990).

The success of *B. straminea* in Hong Kong reflects a high rate of reproduction, at least during the summer months. The mean generation time is only 26 days under optimum conditions in the laboratory, and individuals (which are hermaphroditic) produce 10-70 eggs/day throughout their 20-week reproductive period (YIPP 1983). *Biomphalaria straminea* has a rather generalized diet (DUDGEON & YIPP 1985) and thrives in organically-polluted hypertrophic habitats where other snails cannot persist (YIPP 1990, 1991). Such attributes allow the species to colonize a range of freshwater habitats, particularly those which have been polluted or otherwise altered by human activities.

Poeciliid fishes provide another example where we can relate biological attributes to 'invasiveness'. These animals differ from Hong Kong fishes in producing live young which swim and feed actively from birth, and which do not pass through an unprotected egg phase. Most Hong Kong fishes scatter their eggs or oviposit upon the stream bed; the paradise fish, *Macropodus opercularis* (Belontiidae), is an exception to this and constructs a floating bubble nest containing eggs which are tended by the male. The ricefish, *Oryzias latipes* (Oryziidae) (previously *O. latipes*; UWA & PARENTI 1988), is also unusual in that the eggs are carried in a bunch at the vent of the female until they hatch or are brushed off onto aquatic vegetation. Nevertheless, no Hong Kong fish has the same habits as female poeciliids which store sperm and can produce successive broods of young from a single mating episode.

Poeciliid breeding characteristics reduce predation upon eggs and newly-hatched juveniles, and give solitary impregnated females the potential to colonize new habitats. Carriage of the developing young allows the gravid female to respond to any deterioration in local conditions which may harm the offspring; for example, a night-time sag in dissolved oxygen concentration can be endured if the female rises to the surface to make use of the oxygen-rich surface film. Eggs scattered among the

bottom sediments might perish under these conditions, and it is notable that ricefish and paradise fish have reproductive features which can be interpreted in the same manner, as do the exotic mouth-brooding cichlid *Oreochromis mossambicus* and indigenous snakehead fishes (*Ophicephalus* spp. and *Channa asiatica*: Channidae).

While all four of the poeciliids introduced into Hong Kong have been successful, *Gambusia affinis* is the most widespread and numerous. *Poecilia reticulata* is also widespread, but seems to be declining, whereas the two *Xiphophorus* species (especially the swordtail, *X. helleri*) have relatively restricted distributions. Life-history characteristics seem to explain some of the success of these poeciliids in Hong Kong, and it is instructive to compare *G. affinis* and *P. reticulata* in this respect to account for the changes in the relative abundance of these two species.

An investigation of six New Territories populations of *G. affinis* and five of *P. reticulata* (DUDGEON, D., LAM, P.K.S. & MA, H.T., unpublished observations) has established some of the basic reproductive parameters of these fish, revealing significant intraspecific inter-population variations in condition index (body weight/length), mean embryo weight, total reproductive investment (gonad

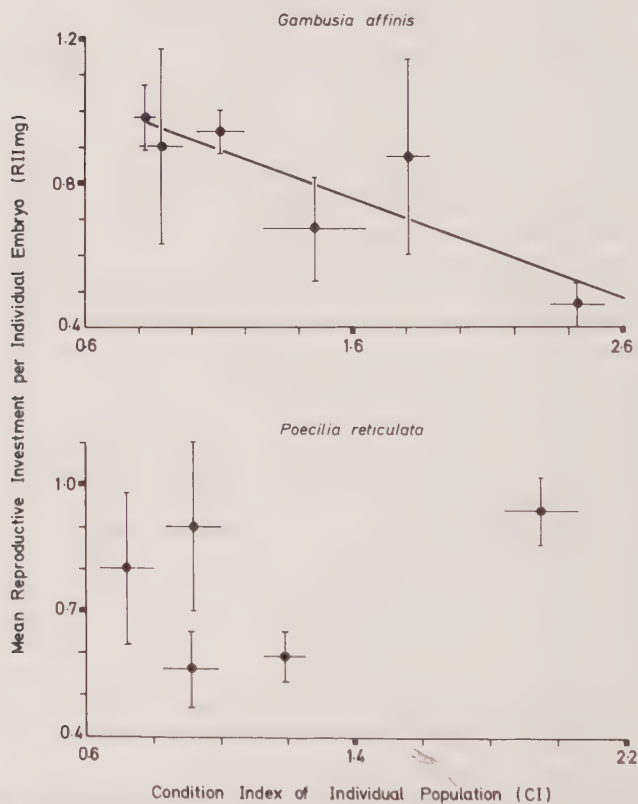


Fig. 40. The relationship between mean reproductive investment per individual embryo (RII mg) and condition index (CI) for populations of *Gambusia affinis* and *Poecilia reticulata*. Vertical and horizontal bars represent standard errors. Best fitting line calculated by the method of least mean squares.

weight/body weight), and the size of breeding females. Can these differences be interpreted as adaptive and, if so, do they provide insight into the success of *G. affinis*?

Variations in life-history traits have been recorded previously for both poeciliids, and can be related to certain habitat characteristics (REZNICK 1981; REZNICK & ENDLER 1982; STEARNS 1983). One such characteristic is likely to be habitat favourability for growth, which can be estimated indirectly from a measure of fish condition index (CI): high CI implies high habitat favourability and *vice versa*. Among the two poeciliids, embryo size (RII: reproductive investment per embryo, mg) increased with declining habitat favourability for growth (decreasing CI) in *G. affinis* but not in *P. reticulata* (Fig. 40). If reproductive investment is fixed or constrained by the need for allocation to somatic growth and maintenance, then producing larger offspring must entail producing fewer of them (SIBLY & CALOW 1985). Furthermore, when adult size is fixed, larger offspring will take a shorter time than smaller ones to reach a size at which they can reproduce (SIBLY & CALOW 1985). Poor conditions for growth are therefore likely to favour larger rather than more numerous offspring, and (all other things being equal) there should be a negative correlation between observed growth or habitat favourability (as indicated by CI) and initial size at birth or embryo size. This correlation is indeed seen among Hong Kong *G. affinis* populations.

It is not known whether there is a genetic basis for interpopulation variations in *G. affinis* life-history traits (and thus they cannot be interpreted uncritically as being adaptive), but the differences are in accordance with some predictions of life-history theory (SIBLY & CALOW 1985). Such agreement suggests that *G. affinis* life-history traits are more 'optimal' than those of *P. reticulata*, and could be invoked to account for the success of this fish in exploiting a range of freshwater habitats in Hong Kong. Significantly, a life-history trait – specifically clonal propagation (asexual reproduction) – has facilitated the spread of water hyacinth and *Salvinia molesta*; if plants are broken apart into separate pieces each has the potential to grow into a complete organism (BARRETT 1989; ROOM 1990). Spread is aided by the high mobility of the plants, made possible by air-filled aerenchyma tissue which gives the stems and leaves of the plants considerable buoyancy. The weeds can therefore float with wind or water currents to unoccupied waters.

Ecological effects of exotic species

Why do exotic species matter to ecologists? Surely, the establishment of exotic organisms is a 'good thing' as it will enhance the species-complement of Hong Kong streams and rivers? The answer to these questions depends upon two things: where the exotic species establish themselves, and what they do when they get there. The second point is crucial; introduced predators can have serious effects, as exemplified by the establishment of exotic piscivorous fishes in tropical and temperate freshwaters (DIAMOND & CASE 1986; WERNER 1986). The introduction of competitors also has important implications for fishes (WERNER 1986), but data on the effects of introductions on other freshwater groups – especially in streams – is scarce.

The direct effects of unplanned introductions may be accompanied by a chain of indirect effects. For example, the piscivore *Cichla ocellaris* (Cichlidae) introduced to

Lake Gatun in Panama eliminated most of the indigenous fish species, increased the number of mosquitoes and certain zooplankton (which had served as prey of the native fishes), and led to a decline the numbers of birds that had fed on the eliminated fishes (ZARET & PAINE 1973). *Gambusia affinis* has been implicated in similar types of indirect interactions: in artificial pools this species reduces macroinvertebrate populations and thereby allows development of phytoplankton blooms (HURLBERT et al. 1972).

Field evidence of the effects of introduced species on the fauna of Hong Kong streams is hard to come by, perhaps because most of the interactions have already taken place. There is circumstantial evidence of the reduction of native fishes by poeciliids, especially *G. affinis* which may act as a competitor with, and a predator of, small fishes. For example, the white-cloud mountain minnow *Tanichthys albonubes* (Cyprinidae) has been eliminated from streams in Hong Kong, while ricefish can be collected only from the few habitats that poeciliids have yet to colonize. In this context it is of interest that the spread of *G. affinis* in Hong Kong appears to have been accompanied by a decline in the abundance of *P. reticulata*. *Gambusia affinis* is pugnacious and, in mixed laboratory cultures, will nip the fins and prey upon the young of *P. reticulata*. The apple snail, *Pomacea lineata* may also owe some of its success to a habit of consuming the eggs and newly-hatched young of potential snail competitors.

The effect of exotic floating plants in streams is likely to be manifested through rapid clonal growth which allows them to cover all or part of the water surface. Reduced light penetration must inhibit the development of submerged plants, and may restrict gaseous exchange between water and air. Water hyacinth roots do provide a habitat for a variety of lotic invertebrates (including gastropods, chironomid larvae, Odonata larvae, Coleoptera, and heteropteran bugs), and the fauna associated with this plant in the lower Lam Tsuen River was more species-rich than that of the bottom sediments (93 versus 19 morphospecies). However, it could be argued that this floating root habitat can be provided by native species such as the water lettuce, *Pistia stratiotes* (Araceae), or replaced by a combination of submerged and emergent plants. Moreover, the species-poor benthic fauna may have been a result of relatively low oxygen concentrations beneath the Lam Tsuen River water hyacinth beds, perhaps reflecting an influence of the dense mats of floating plants on gaseous exchange at the water surface. Overall, the benefits derived from exotic species do little to outweigh the accompanying costs.

Where are exotic species most successful?

Clearly, the habitats where introduced species establish themselves are those which are most susceptible to invasion. The main criteria determining such susceptibility are the species richness of the receiving community (invasion success declines steeply with species richness of the extant flora and fauna), and the number of recent extinctions (the more recent extinctions there have been, the greater the chance of an invader's success) (ELTON 1958; DIAMOND & CASE 1986). These attributes probably affect the intensity of competition or predation that the exotic species will experience upon arrival, and there is a circumstantial link between resistance to invasion and the diversity and abundance of native species (DIAMOND & CASE 1986). Note that there is a strong interaction between an invader's likelihood of

success and what it does upon arrival; an introduced predator will have more chance of success than an introduced herbivore, because the latter is more likely to experience predation from the native fauna.

All of the successful invasions of Hong Kong running waters have occurred in lowland streams. These habitats are perturbed by man, and pollution as well as flow regulation may have eliminated native species. Alteration of habitat characteristics and the loss of native species provide an opportunity for establishment of new invaders, and the features of some of the exotic species (high rate of population increase and tolerance to organic pollution in *Biomphalaria straminea*, flexible life-history traits in *Gambusia affinis*), seem to have 'preadapted' them to disturbed habitats. Exotic species have failed to establish themselves in hillstreams – a reflection of the fact that such streams are relatively unperturbed, and hence possess a full complement of species making them rather resistant to invasion (DIAMOND & CASE 1986).

Is there reason for concern over exotic species?

Biological invaders differ from native species in resource acquisition and/or resource-use efficiency. They can alter the trophic structure of an invaded area, and may compete with or consume native organisms. In so doing, the exotic species affect ecosystem- or community-level processes such as primary or secondary productivity, decomposition, and nutrient cycling. The properties of invading species can therefore control ecosystem functioning and thus alter the fundamental rules of existence for all organisms in an area (VITOUSEK 1990). Clearly, there are good reasons to be concerned about exotic species in Hong Kong.

All of the successful invasions of Hong Kong streams have occurred in lowland habitats, and it is in these sites that the native fauna suffers most as a result of human activities. The introduction of potential competitors or predators is yet another nail in the metaphorical coffin that is being fashioned for this component of the running-water fauna. Such introductions must, therefore, be deplored. It is probably too late to return our running waters to their aboriginal state by eliminating the invaders. Extermination of widely-distributed species would, at any rate, be impractical. Nevertheless, we should make every effort to ensure that they are not added to by further introductions. In addition, it is important to guard against spreading the existing exotic species further afield where they may jeopardize other communities.

The future

There is room for optimism in that Hong Kong hillstreams retain a diverse fauna. The reliance placed upon streams as a source of water in Hong Kong has ensured the protection of uplands – and the running waters draining them – as catchment areas. Notwithstanding, the use of streams to provide water for a burgeoning population has the disadvantage that much of the flow to the lower reaches is diverted into tunnels and storage reservoirs. This water transfer affects the ecology of lowland streams and rivers profoundly, and the deleterious effects are magnified many times

by the pollution loads that the habitats receive. In these perturbed rivers and streams, exotic species have established themselves and flourished. It may never be possible to determine whether interactions with these exotics or habitat degradation has been responsible for the decline or loss of species from lowland streams; indeed, the interaction of these factors is likely to be more damaging than the simple sum of their effects. Although government is taking steps to reduce the input of livestock wastes into rivers, the rapid population growth and development of the New Territories do not augur well for the future of Hong Kong's running waters. Moreover, whether government can increase and then sustain environmental protection efforts in the face of the political changes that Hong Kong will undergo is an open question.

V Synthesis

The analysis of Hong Kong stream ecology at three levels of integration – individuals, populations and communities – demonstrates how the attributes of individuals (foraging behaviour, morphology, growth, and so on) combine to generate population characteristics which, in turn, blend to produce spatial and temporal variations in community composition. These variations may involve downstream replacement of species along the length of a river, or seasonal changes in stream drift and benthic community composition at a single site. It is the attributes of individuals and populations which determine the timing of breeding by aquatic insects, but adult emergence, mating, and subsequent recruitment of juveniles affects community composition by altering species relative abundance. The tolerance of the individuals making up a population to pollution-induced stress will also have implications for community structure, especially when – as in Hong Kong – pollution loads vary with the seasons.

Seeking an explanation for patterns observed at one level of integration by looking towards lower levels is typical of the reductionist approach of conventional science. Here we are saying that it is necessary to examine component parts before we can understand the behaviour of a complex whole; we are not saying, however, that the features of the whole are nothing but the simple sum of the component parts. This point is easily understood with reference to the traits of each level of integration. Communities, for example, have the emergent property of species diversity – a feature which has no counterpart at the population level. Similarly, populations of dioecious species have sex ratios, but an individual is either male or female. The reductionist approach is therefore necessary and useful as a means for understanding patterns and processes in terrestrial or freshwater habitats, but cannot always be employed in an uncomplicated, additive fashion to provide a complete description of those patterns or processes. Ecological phenomena have an evolutionary and historical dimension, and hence may not be interpretable from observations of present-day circumstances. Nevertheless, a genuine understanding of ecological systems (which provides a basis for predictions of the effects of habitat perturbations or management strategies) must rest on explanations derived from the properties and behaviours of the constituent components: *viz.* communities, populations and individuals.

The investigation of exotic species provides a good example of how different levels of biological integration are linked. Where individual species invade and alter habitats by eliminating native species, population-level process – based on the individual properties of the invader – become community- or ecosystem-level processes. When ecosystem properties are altered by invasions, all organisms are affected because the basic rules of life in that habitat change.

One difficulty with the reductionist approach arises from a tendency to over-simplify ecological interactions. It is fairly obvious that colonization of a stream by n populations will not lead to the development of a community comprising n species but one containing $n - ?$ species. Some of the original colonizers could be predators which might eliminate one or more vulnerable populations; individuals of other populations may compete with each other leading, in extreme cases, to the exclusion of all members of subordinate populations. Still others may colonize the habitat, yet be unable to breed and persist there under the prevailing physical regimen. Clearly, to predict the community structure which would arise from a known pool of colonizing species we have to know about the attributes of each population; specifically, their feeding habits, competitive hierarchies and tolerances.

Even with such information to hand, community composition cannot be predicted with any certainty. The nature of the physical environment – the habitat template – will affect the outcome of interspecific interactions. A cobble stream bottom, for example, will alter the efficiency with which a predator captures prey when compared with a sand sediment, and both the predator's response to substrate and the ability of prey to use it as a refuge must be taken into account (FULLER & RAND 1990). Water-quality can affect prey vulnerability (CLEMENTS et al. 1989), and the presence of alternative quarry also influences the outcome of a particular predator-prey interaction, as demonstrated for the crab *Somanniathelphusa sinensis* which eats certain gastropods when they are presented alone, but rejects them when given a choice of prey. Investigations on Hong Kong stream invertebrates have also shown that foraging behaviour is affected by prey density (in *S. sinensis* and *Diplonychus rusticum*) and hunger (in pulmonate snails), indicating that individual differences among members of a population may affect the outcome of interspecific interactions.

In most cases it will probably be inappropriate to attempt to predict the dynamics and interactions of a population by assuming that the component individuals are identical. A population model which combines many individuals under the assumption that they can be described by a single variable, such as population size, is doomed to failure. The deficiency lies in the fact that each individual is different, with behaviour and physiology that arises from a unique combination of genetic and environmental influences. Moreover, a population model that ignores the location of organisms will have little predictive power because it contains the assumption that each individual has an equal effect on every other one. This is untrue since interactions are inherently local, and individuals are affected primarily by others with which they come in contact (HOUSTON et al. 1988). Interference competition between filter-feeding blackfly (Simuliidae) larvae and net-spinning, sedentary Hydropsychidae in streams provide a good example of such local interactions (HEMPHILL 1988). In short, the original age- or size-distribution and dispersion pattern of the individuals constituting a population will affect the outcome of both intra- and interspecific interactions (HOUSTON et al. 1988). Assumptions that all individuals are statistically similar and that each interact uniformly with all other members of the population are ignoring reality. Further complexity is introduced when we take cognisance of the fact that many ecological phenomena are non-linear, and even the simplest population models produce chaotic dynamics under certain starting conditions (MAY 1986).

Under most circumstances, it is clear that the individual is the proper basic unit for describing ecological phenomena (FRYER 1987; HOUSTON *et al.* 1988), and our understanding of stream habitats will come only with a greater appreciation of the factors determining the fitness parameters of individuals. This does not mean that we cannot find regularities, rules or patterns at the community or population levels, but that for full comprehension we must not gloss over the variability which lies at the heart of ecological systems. A true comprehension of many biological phenomena (especially in ecology where numbers are easily generated) may require qualitative rather than exclusively quantitative knowledge (FRYER 1987).

Should we abandon the study of stream communities, and concentrate our attention upon investigations of individual stream organisms? That approach is to throw out the baby with the bath water. Work on Hong Kong streams has demonstrated that investigations at the community level – for instance, an examination of the effects of riparian vegetation on benthic communities – reveal interesting patterns that reflect changes in the trophic structure of streams. A shift in the balance between autochthonous and allochthonous food sources alters the relative abundance of populations (and functional feeding groups) and affects community structure. While we have much to learn about the feeding habits of individual species (and different developmental stages within species), our inability to detail trophic relationships in no way invalidates the conclusion that riparian vegetation has a profound influence on stream ecology, and such information can still be used to formulate appropriate management strategies for lotic habitats. It is worth noting here that the River Continuum Concept is based upon a recognition of community-level patterns, rather than depending upon a bottom-up approach focusing on individual organisms. Although not without detractors, the Concept does provide a useful heuristic framework and has stimulated research aimed at testing the generality and causes of downstream changes in river communities.

One obstacle to a fuller understanding of stream ecology is the nature of interactions in lotic habitats. Traditionally, mechanisms controlling community structure have been viewed as deterministic: with a knowledge of the starting conditions we can predict a particular outcome. More recently, stochastic processes have moved to centre-stage with the consequence that we no longer predict a single outcome based on a set of starting conditions, but instead indicate a variety of possible outcomes each with a specified chance of occurrence. The latter procedure is 'biologically reasonable' as it mirrors our approach to the study of individual organisms. That is, we say that an animal has a particular chance or probability of surviving for one month or attaining maturity, and reproduction is likewise expressed in terms of the probability of breeding and the relative chances of producing one, two, or more offspring. The introduction of chance complicates ecological modelling and prediction, but mimics natural processes.

Chance or probability makes a dramatic appearance in Hong Kong streams through the action of periodic disturbances such as the spates associated with typhoons or monsoonal rains. Floods associated with seasonal rains are characteristic of rivers throughout the Oriental tropics (DUDGEON *in press*), influencing land-water interactions, life-cycle events, and so on. Spates in particular cause mortality through scouring, washout, or animals being crushed by shifting rocks. The stream bed is physically disrupted, sediment characteristics change due to the

export of fine particles, and the availability of microhabitats is altered. An individual's chance of surviving such spates cannot always be predicted from biological attributes, and the subsequent growth and reproduction of that individual (and hence of the species population) depends upon the availability of food and microhabitat, as well as whether or not predators and competitors perished during the spate. Recurring disturbances of varying intensity will disrupt biotic interactions in streams. Accordingly, a deterministic projection that species *a* will eliminate species *b* by eating it, or that species *b* should exclude species *c* by competition, will be misleading if populations of the predator or superior competitor are periodically reduced by spates. There is growing awareness of the role played by disturbance in streams (HILDREW & TOWNSEND 1987; RESH *et al.* 1988), but there is a great deal to learn. One issue is to relate changes in community structure to community functioning, the latter forming a cornerstone of the River Continuum Concept. Disturbance may cause a change in species representation but, if species lost are replaced by others of equivalent habits, community functioning will not be disrupted. For example, loss of members of one functional group and their replacement by other species of that group will change community structure only. Their replacement by representatives of a different functional group will, however, affect community processes and functioning. It is important that we should be able to distinguish between these possibilities, especially where man's activities have caused changes in stream community structure. Restoration of damaged habitats must address the problem of reestablishing community functioning even where the original species composition cannot be emulated.

Progress in understanding Hong Kong streams will be made most rapidly once we are in a position to frame and test appropriate hypotheses unambiguously. Such investigations can be undertaken on individual animals (often in the laboratory), and studies of foraging behaviour and prey selection provide representative examples. However, without prior observations on populations and communities in natural habitats, we cannot know what questions to ask and which hypotheses to test at higher levels of integration. If we lack the knowledge to answer basic questions concerning the seasonality, population dynamics, productivity and life-history patterns of common stream organisms, and if we do not know the extent of inter-stream and year-to-year variations in these and other ecologically-relevant factors, then we cannot know which hypotheses will be relevant or significant and tractable.

Like many other areas of scientific research, work on tropical running waters lags behind investigations of their temperate counterparts. Experimental studies in stream ecology are particularly rare in Asia (but see BENZIE 1984 and DUDGEON 1991a, 1991b). There is still a great need for descriptive research that will reveal the general characteristics of the habitats with which we must work. The relevant research must be carried out as a matter of urgency because the rate of degradation of tropical streams and rivers is alarming. Moreover, our need to protect and manage these habitats is hampered by a lack of knowledge of tropical systems. Although some ecological phenomena may be universal, with latitudinal differences manifested in matters of degree rather than kind, we must be careful not to assume that tropical streams and rivers are nothing more than warmer versions of their temperate analogues. There may be imbalances in our perceptions of the ecology of inland waters arising from an excessive concern with the northern temperate region.

As a result, many widely-held limnological concepts may be erroneous and in need of revision (WILLIAMS 1988). Moreover, HYNES (1989) has pointed out that few large rivers are left for study in anything like their original condition, and thus work on the few near-pristine tropical rivers that remain (e.g. WELCOMME 1979) may have important lessons for temperate-zone limnologists.

The rate and extent of destruction and perturbation of tropical habitats in general, and streams in particular, means that we cannot afford to scamper back to our laboratories and field sites to spend decades developing latitudinally-relevant paradigms for tropical freshwater ecology. Moreover, once armed with appropriate hypotheses, we may still find ourselves faced with practical and moral barriers when it comes to testing them. How, for example, can we justify experiments on a scale involving clear-cutting a tropical rain forest or poisoning a pristine stream when we wish to test a hypothesis concerning interactions between the stream and its valley? 'Hard' science (based upon experimental methodologies) and tight causal proof are not the only bases for instituting controls to protect streams and rivers from degradation. The immediate practical issue is to preserve these habitats from irreversible impoverishment. The tools we have to work with are fewer data or concepts than we would like but, at least, a degree of experience. Our effective stewardship of these habitats and biota will depend to a great extent on this ecological experience combined with common sense and intuition. It is long past time that we emphasized the inadequacies of current knowledge (WOODWELL 1989). The biota is finite in our time and under current management, but potentially an enduring resource. Nit-picking, hyper-objectivity or inaction because of a shortage of data will result in the squandering and impoverishment of our common heritage and the subject of some scientists' life-work (WOODWELL 1989). While no one would counsel abandoning the strictures of objective scholarship, it would be folly to surrender streams and their biota to those who would degrade and pollute them while scientists gather more data.

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